PRINCIPLES OF AGRICULTURAL BOTANY

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PREFACE

THE agricultural student of to-day may expect to see farming under a wide diversity of natural conditions. As he moves about, the knowledge he will find most useful in new situations or under unfamiliar circumstances is a knowledge of principles. The material included in this book has been selected with this requirement in mind, but local applications of botanical science have been described for purposes of illustration.

It seemed to the author that he could best use the strictly limited space at his disposal by eliminating as far as possible descriptions of what the student should see for himself, and it may appear that some subjects have received rather cavalier treatment. No attempt has been made to trench on the studies which should more appropriately be carried out in the field or in the practical laboratory. Nevertheless, matters of botanical interest significant in agriculture have received adequate treatment.

I am grateful to many friends all over the world for providing many photographs ; these have been acknowledged in the appropriate place. Miss B. D. Inglis provided all the line drawings of plant material, and the Colour Plates X and XV ; to her I am especially grateful. My thanks are due to my two friends and colleagues, Dr. Janet F. A. Maclagan and Mr. John Anthony, who have read the proofs. Finally acknowledgment must be made to the publishers, whose enthusiasm has made the book possible.

A. N.

University Department of Botany
at The Royal Botanic Garden
Edinburgh *June*, 1946

TO THE STUDENT

THIS book has been planned and written with two main objects in view. First, to put before you those principles of plant science that bear on Agriculture, along with some examples of the application of them to farming practice. Secondly, to assemble all the information likely to be required by you when preparing for a formal examination in Botany, leading to a degree or diploma in Agriculture.

How to Use the Book. Read the text through. Do not attempt to master detail, but rather try to see the pattern botany makes as it seeks to serve world agriculture. When this reading has been completed study different parts of the text in an order different from that adopted here, so that new relationships are formed between the various sections and chapters. Relate what you read to what you see in the laboratory and field.

Do not try to remember words. Visualize what the words mean ; clarify and sharpen the mental images you form by making drawings ; write précis of what you have read.

Work in the Laboratory and Field. Plant science consists very largely of the recognition of plants and parts of plants, and of the effects of peculiar conditions on plants. This branch of the subject cannot be learnt satisfactorily from books, no matter how profusely they are illustrated. In this book, the features used in identifying plants have been defined and the methods of using them indicated. You yourself must see, draw, describe, and as far as possible experiment until you recognize a specimen or phenomenon in the same way as you recognize an acquaintance—by familiarity. This aspect may be summed up in these words, " Seek for practical experience."

Preparing for an Examination. In preparation for this narrower part of your work, first see a syllabus of the examination, and read through questions set on previous occasions. This should direct your detailed studies along suitable lines. During these studies the writing of simple précis covering selected parts of the subject will focus your attention, and later aid your memory.

Further Work in Botany. After you leave college and your professional career develops, more data than can be included in a general text will be required. As a guide to further reading, a list of books more specialized in character is appended to each chapter. Up-to-date information should be obtained from

original papers reporting new research. Abstracts of these are given in a number of publications, and a list of Abstract Journals is appended.

Keep abreast of the general trends of agriculture by reading the periodical press which serves our industry so well. The publications of your Department of Agriculture will also help you.

In all your reading and study be critical. When statements made by authorities appear to conflict with one another or with observations of your own, you should refer to the object itself, to experimentation, or to the practical man on the land, who often has the facts though perhaps not the scientific explanation.

ABSTRACT JOURNALS WRITTEN IN ENGLISH

Biological Abstracts. Sponsored by the Union of Biological Societies of America, Philadelphia

Experiment Station Record. Issued for U.S. Department of Agriculture by U.S. Government Printing Office, Washington, D.C.

Horticultural Abstracts. Issued by Imperial Bureau, Horticultural and Plantation Crops, East Malling, Kent

Plant-breeding Abstracts. Imperial Bureau of Plant-breeding and Genetics, Cambridge

Herbage Abstracts. Imperial Bureau of Pasture and Forage Crops, Aberystwyth

Soil and Fertiliser Abstracts. Imperial Bureau of Soil Science, Harpenden, Herts

Forestry Abstracts. Imperial Forestry Bureau, Oxford

The Review of Applied Mycology. Imperial Mycological Institute, Kew

The Bibliography of References to the Literature of the Minor Elements. Issued by the Chilean Nitrate Educational Bureau, 120 Broadway, New York, or Stone House, Bishopsgate, London

CONTENTS

SECTION ONE

MORPHOLOGY AND ANATOMY

SECTION TWO

PHYSIOLOGY

SECTION THREE

NEGATIVE FACTORS IN FOOD PRODUCTION

(WEEDS ; INSECT PESTS ; DISEASE)

SECTION FOUR

HEREDITY, EVOLUTION, AND CLASSIFICATION

COLOUR PLATES

All these plates except Nos. X, XV, and XVII are reproduced from colour photographs by Mr. T. C. Dodds, F.I.M.L.T., F.I.B.P., F.R.P.S. Plate XVII is by courtesy of Dr. E. G. Mulder.

BLACK AND WHITE PLATES

BLACK AND WHITE PLATES

SECTION ONE

MORPHOLOGY AND ANATOMY

After a brief discussion of what is meant by food and the importance of the plant as a food-making organism, this section deals with the appearance and construction of a typical green plant.

There are two main divisions in such a study—Morphology, the study of outward form, and Anatomy, the study of internal structure. Study of the fine anatomy of the ultimate units of construction—the cells—is called Cytology.

All these will be dealt with here, but only in so far as they serve useful ends either in understanding how the plant works, or in identifying the different plants or parts of plants which are important in agriculture.

Chapter I

FOOD IN GENERAL AND ITS SEVERAL KINDS

Green plants make their food from materials which are not themselves food. This synthesis is the basal activity of the agricultural industry. Animals can only change the character of that on which they feed; no animal can carry out the primary synthesis. All agriculture then depends upon the successful exploitation of the food-making capabilities of the green plant.

The water, gas, and manures which the plant absorbs from outside and uses cannot be regarded as food; their energy content is nil.

Plants and animals live on exactly the same kinds of food. Man and the herbivores merely consume the bodies of plants or the stores they have made and accumulated for their own use.

Food is defined as "all those substances which can be used by a living organism as a source of energy or for the formation and repair of body tissues."

The Several Classes of Food

Within this definition three main classes of material are recognized. These are carbohydrates, fats, and proteins. There are other essential components of a complete diet, vitamins, minerals, etc., but none of these are required in quantity, nor are they so fundamental in character, and indeed may not be food within the terms of the definition.

The three big classes are not of equal value in the sustenance of the living organism. On the basis of the energy they supply, carbohydrates yielding 4·15 calories per gram are not so valuable as proteins giving 5·65 calories per gram, and these in turn are surpassed by fats with an energy content of 9·4 calories per gram.

In so far as food is regarded as a source of energy this standard of value may be regarded as valid, but when the functions of body-building and tissue repair are considered the order of merit alters.

Proteins are of greatest value to the living organism, because they are the essential components of the actual living material—

protoplasm. No life is possible in the absence of protoplasm, and it is a complex mixture of different proteins. Protein is difficult to synthesise and has a special scarcity value. It is the most complex foodstuff the plant produces, and requires for its formation an adequate supply of nitrogen and other elements which are often in short supply.

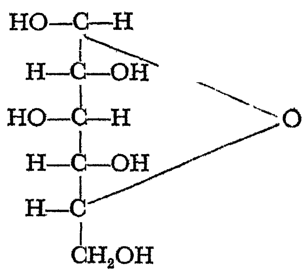
Carbohydrates are "cheap" to produce but bulky to store. They may be valued against fats, which are more difficult to produce and more concentrated, entirely on relative energy content.

CARBOHYDRATES

Consider now what these foodstuffs are and how they are used. The simplest are the carbohydrates. They contain in their molecules only carbon, hydrogen, and oxygen. The hydrogen and oxygen are present always in the proportions they show in water, two of hydrogen to one of oxygen. Hence the name hydrates of carbon or carbohydrates.

Within the carbohydrates the simplest member manufactured by the plant contains in its molecule six atoms of carbon, twelve atoms of hydrogen and six atoms of oxygen. This may be written $C_6H_{12}O_6$. These atoms in the molecule are not arranged in space in any haphazard fashion, but in very definite ways. For example, the carbons always form a chain with the hydrogens and oxygens disposed about them laterally.

As for example :



A form of Hexose

This is the best representation of a molecule possible on a plane surface such as a printed page. It must be remembered that these molecules are three-dimensional bodies, and in the example shown the constituent groups are distributed round the

carbon chain. The formula given is merely a projection. The photographs of models shown in Fig. 1 give a more accurate impression of the actual structures.

Isomerism

The point of importance, however, is that if there is any change in the spatial relationship of the various components, (H) or (OH) groups, the substance alters in some of its characters such as sweetness, solubility, and so on. As there are many possible arrangements of these groups on the six-membered carbon chain, there are many possible substances having the formula $C_6H_{12}O_6$, all of which possess individual characteristics. Substances which have the same elements in their molecule, in the same proportions, but show different properties due to different groupings or different arrangements in space of similar groups, are called isomers. Of the many possible isomers of $C_6H_{12}O_6$ only two occur commonly in plants. These are glucose and fructose. It will be noticed that both those names end in " ose." This termination should be used in naming the simpler carbohydrates and many of the substances built up from them but containing in the molecule no other additional component. The members with six carbon atoms then may be termed the hexoses.

Condensation

When two hexose molecules come together under appropriate conditions, one can lose a hydrogen (H), and the other a hydroxyl (OH) group, while the two main bodies join through the valence bonds so set free. Thus a large molecule, nearly double in size, with the general formula $C_{12}H_{22}O_{11}$ is formed and water HOH thrown out.

Similarly three hexoses can form a " three times " molecule $C_{18}H_{32}O_{16}$ and two molecules of water are thrown out.

This ability of simple carbohydrates to act as a group or radical and form more complex molecules without the introduction of a new component is called condensation. For this reason the hexose molecule is called a monosaccharide while the twice hexose $C_{12}H_{22}O_{11}$ sugars are the disaccharides.[1] Both classes are included in the general term " sugars."

[1] If the terminology were standardised the various carbohydrate groups would be called saccharoses. An appropriate prefix would be added, *e.g.* monosaccharose.

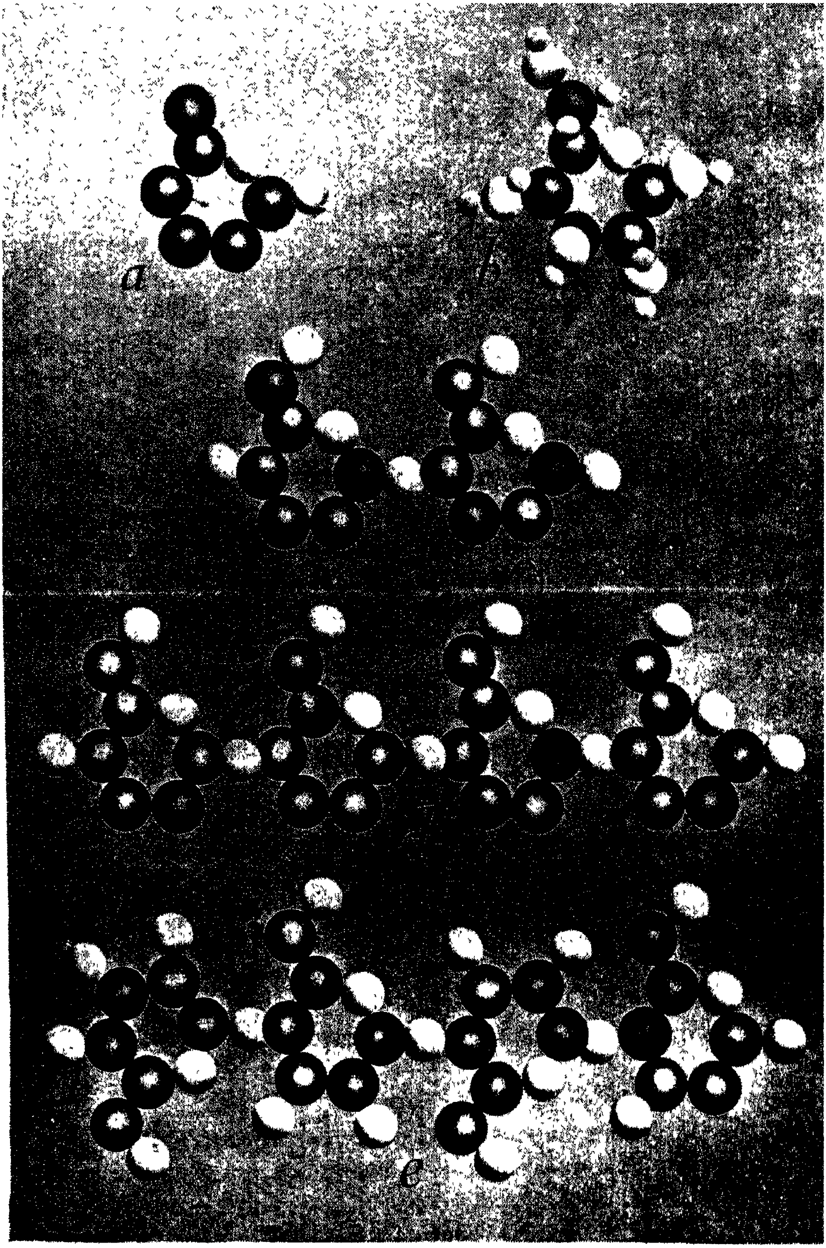


Fig. 1

Models illustrating the structure of carbohydrates; black spheres are carbon, large whites are oxygen, and small whites are hydrogen

(*a*) "Skeleton" of glucose (*b*) complete glucose (*c*) maltose "skeleton" (*d*) starch "skeleton" (*e*) cellulose "skeleton"

The higher and more complex members similarly take a prefix appropriate to the number of monosaccharide groups included in their molecule.

In nature the plant forms first mono- and then perhaps disaccharides. Trisaccharides are rarely formed. The next stage in condensation is when many hexose molecules are used to form a large molecule called a polysaccharide. The plant, instead of making the polysaccharides from monosaccharides by a step-by-step process, adding one hexose at a time, seems to take many monosaccharide molecules simultaneously and form the larger molecule directly.

The polysaccharides have a molecule represented by $(C_6H_{10}O_5)_n$ or more accurately as $(C)_n(H_2O)_{n-1}$ when n is a high number, probably never less than 30 and often more than 200.

Hydrolysis

Just as the complex polysaccharide molecule is built up by the plant with apparent ease, so too is it broken down. Quite slight alterations in conditions can change the process of condensation, with water being discarded, to a process of breaking down with replacement of water in the molecules. This process of re-formation of monosaccharide units from one of the higher forms takes its name, hydrolysis, from this fact that water has to be broken into two parts, (H) and (OH), and these fixed into the separate derivatives.

Condensation and hydrolysis are processes quite opposite in effect; one, the building-up of complex molecules from relatively simple units; the other, the breaking down of the complex to the simple. The value of this mechanism to the plant is seen when the differences in character of the different grades are studied.

Monosaccharide molecules are relatively small and very soluble in water. As will be shown later they can be moved about in the plant quickly and with comparative ease. Thus they may be rapidly transferred from one part of the plant where they are many to another part where they are few.

This mobility, and the fact that they provide a very quickly available source of energy, makes them very useful.

On the other hand the occurrence of high concentrations of monosaccharide molecules may be a danger to the maintenance

of physical balance in the cells and tissues. By condensation to disaccharide the number of molecules present is reduced to half, and the solubility of these molecules is less.

Thus condensation of a mono- to disaccharide reduces the risk involved in having many molecules in solution at once, while at the same time not reducing by much the availability of the material as a source of energy.

When sugar synthesis is rapid and the concentration of mono- plus disaccharide reaches dangerous levels, condensation in many plants is carried further to form polysaccharides. Commonly these are starches and celluloses, which are practically insoluble. Being insoluble, they are almost completely inert physically.

Starch

Starch locks up a store of energy which can be kept indefinitely. Later, hydrolysis will reform the monosaccharide for use *in situ* or translocation as, and where, and how required. Starch then is a practically inert reserve substance readily rendered available for use when required.

Cellulose

On the other hand, monosaccharide derived directly from synthesis or from hydrolysis of stores can be built up into cellulose. Cellulose differs from starch fundamentally only in that the arrangement of the monosaccharide units in the large molecule is different This alteration in arrangement of the units renders cellulose not only insoluble but also not easily hydrolysed. It also confers on the material considerable tensile strength. Thus cellulose is the basic material for constructing the "skeleton" of the plant. Walls in their many forms in the plant are first laid down as cellulose.

The Carbohydrate Flux

The picture suggested is one of the plant synthesising comparatively simple units, the monosaccharide molecules. The units, usable in themselves as an energy source, are also equally important as "building bricks." By the process of condensation the bricks may be piled up in a compact molecule as starch for use in the future, or they may be arranged into the more permanent molecules of cellulose to form the skeleton of the plant.

Thus by condensation and hydrolysis the carbohydrates are

in flux either in up-grade from simple to complex or down-grade from complex to simple, the direction taken depending on conditions within and without the plant.

Addition Compounds of Cellulose

It will be convenient to note here that the characteristics of cellulose in the plant are usually modified by the addition to the wall of another component derived from less well understood syntheses. For example, a wall of pure cellulose may be rendered impermeable to water by the deposition on its surface of molecules of an oily character. This is in effect very like the application of paint to the walls of a house. Again, molecules of other substances such as lignin, a highly complex aromatic alcohol, may be introduced into the walls between the monosaccharide units and alter its characteristics. This is analogous to putting material in the spaces of hollow-brick walls of a house.

Summary: The Various Uses of Carbohydrate

In summary form it may be said the carbohydrate flux and modification of its members provides an energy source, units of transport, skeletal material, and reserves for any or all of these. Finally, some form of carbohydrate is the basal material for the synthesis of almost all other compounds in the plant.

FATS

Fats differ fundamentally from carbohydrate in that there is less oxygen in the molecule. That is to say, they too contain only carbon, hydrogen, and oxygen, but the oxygen is in a smaller proportion to the hydrogen than is found in water.

Having less oxygen in the molecule increases the proportion of carbon and hydrogen, the oxidisable material, and hence unit weight of fat provides more energy than unit weight of carbohydrate. Fat is a more concentrated source of energy. Fats occur in the plant as oil. Oils differ from fats only in having a lower melting point and are therefore liquid at normal temperatures. In the plant they occur as droplets in the sap. They provide a concentrated form of energy, and are invariably used as stores or reserves usually in situations such as a seed where

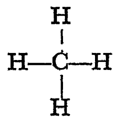
space is restricted. When the reserves have to be drawn upon oils must first be converted back to carbohydrate, so that they are not so readily available when required.

Proteins

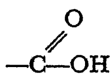
Protein molecules are very large and complicated. They are built up by a method analogous to that by which polysaccharides are formed though the units employed are more varied in character than monosaccharide. How the basal units of protein are synthesised is not well understood, but how they condense is quite clear. The units are molecules of amino-acids.

The Structure of a Simple Amino-acid

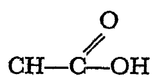
There are many different kinds of amino-acids. Theoretically they may be regarded as derived in the following way. Let us commence with an alkyl group, and here we will use methane, the smallest and simplest, as our example. This substance may be represented as CH_4 or structurally as :



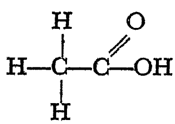
By appropriate manipulation each of the hydrogens may be replaced by other groups. One which may be used in this way is the carboxyl group



This group when present in a molecule confers an acid character; it is typical of organic acids. Hence, if the compound

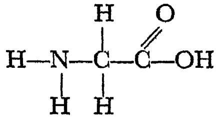


or structurally :



is made, the compound is acetic acid.

Another group which may be used to replace another hydrogen of the alkyl is (NH_2), the amino group. Like ammonia, to which it is related, it is highly basic in character. This gives a compound CH_2NH_2COOH, or structurally :

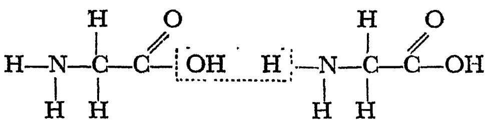


which is amino-acetic acid or glycine.

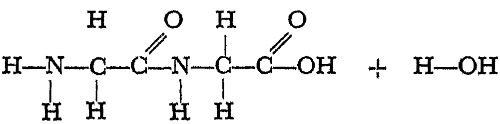
Condensation of Amino-acids

It will be noticed that this molecule is so constructed that it is basic at one end of a carbon chain and acid at the other. Having such a constitution it is called an amphoteric compound, *i.e.* one having a double nature.

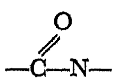
If two of the glycine molecules are brought together in a suitable way the acid portion of one reacts with the basic portion of the other, and water is eliminated. This is seen in this way :



and the compound which results is glycylglycine :



This compound is still amphoteric, having an acidic group at one end and a basic group at the other. This condensation can go on till the very big protein molecule is built up. It will consist of amino-acid units linked through the special linkage



At every link of this kind one molecule of water will have been eliminated.

Hydrolysis of the Peptide Linkage

In nature the breaking (hydrolysis) of this linkage is commonly carried out by an agent called pepsin. Therefore it is called the peptide linkage, and is the fundamental link in all proteins.

The point it is desired to make here is that proteins are hydrolysed with comparative ease in the same way as carbohydrates, and that the building units are always amino-acids.

Complication of the Proteins

There are many different organic acids, and depending on the nature of the one involved, amino-acids differ considerably amongst themselves. Further, any number of the side hydrogens may be replaced. Many different groups may enter into these replacements, and the presence of each confers on the amino-acid concerned other and often potent characteristics. Inclusion or omission of any one amino-acid or variation of it changes the nature of the protein so formed. The character of the protein built from this very varied set of bricks also changes if the number, or the order in which different members come on the chain, is altered. In short, the possibility exists of many millions of different proteins. The marvel of the chemistry of the plant is that any one kind of plant, generation after generation, always builds the same kinds of protein.

The Living Plant

Definition of what is meant by living, and what by plant, is not easy. In fact, living can only be defined by reference to the characteristics shown by something which is alive. Anything which is alive exhibits six different activities or functions all working together and organized into a harmonious whole. This ability to organize is taken as the mark of living-ness, for when it disappears disease and death follow.

The Primary Functions

The six primary functions of the organism may be listed :

(1) The living plant takes from its environment material chemically unlike itself. This it refashions so as to build up its own substance. It is said to *feed.*

(2) By a controlled process, analogous to combustion, energy is released from the substance in the body. In short, the organism *breathes* or respires.

(3) The excess of material from the building-up process of feeding over the breaking-down process of breathing is used to increase the size of the body, and the organism is said to *grow*.

(4) In time, new and different units of structure or organs are added to the body, and it is said to *develop*.

(5) Life doubtless originated in a water medium, and the necessity for water is a heritage of everything that is alive, it must *imbibe*.

(6) Finally, living things by a process more complex than simple division or fission reproduce their kind. They are said to *reproduce*.

The *green* plant, as has been said, adds a seventh and most important ability, that of being able to manufacture its own food from material that is not food, using light as a source of energy.

By understanding each of these functions, manipulating and controlling them, primary food production may be exploited to the best advantage.

BOOKS FOR FURTHER READING

WINTON, A. L. and K. B. *Analysis of Foods* (John Wiley & Sons, Inc., New York ; Chapman & Hall, Ltd. London)

PLIMMER, R. H. S. *Organic and Bio-Chemistry* (Longmans & Co., 1938)

THATCHER, R. W. *The Chemistry of Plant Life* (M'Graw-Hill Book Co., Inc., New York, 1921)

CHAPTER II

THE GREEN PLANT: MONOCOTYLEDONS AND DICOTYLEDONS

FROM what has been said in Chapter I, the chief interest of agriculture is directed to green plants. A great many kinds of these exist in the world to-day. Some are quite simple in structure, being formed from only one unit or cell. Others show great complexity of body, being composed of many thousands of individual cells all working in harmony. Between these two extremes all degrees of complexity may be seen.

EVOLUTION

Such a sequence is believed to be the result of a process of evolution, whereby a simpler form acquiring a new part or ability gives rise to a new and higher degree of complexity.

A similar sort of process may be seen in human affairs. The simple kite such as boys fly provided the aerofoil. Kites of varying complexity developed, and the glider eventuated. Provision of an engine led to the development of the many forms of the powered aeroplane. At every stage, any development which on trial did not render the "plane" more suited to the purpose would be rejected and so eliminated from the stream of development. Only the "useful" would persist. These three major types of air-borne structure are alike in principle but differ in many ways, and each has given rise to many variations, but definite lines of evolution and a degree of relationship can be seen connecting all forms from the simple kite to the modern air liner.

Organic Evolution

Amongst living things from time to time new types arise, not from man's invention, but naturally. When one of these variations occur, if the individual showing it develops better, survives longer, or reproduces more profusely, in fact is able to compete successfully with its contemporaries, it tends to become predominant over them. It is said to succeed in competition because it is more fitted to survive in the particular environment involved.

Plant Introduction

Two general concepts may be derived from this. Firstly, that the plants occurring naturally in any area will tend to be the types most suited to the environment there. This concept underlies the principles governing the decision as to which crops should be grown in a newly settled country. Similarly it determines which kinds are likely to succeed when introduced into one country from another. Usually plant introductions are made from one area to another of somewhat similar environment. Evolution, however, may have taken place faster and gone further along particular lines in the one area than in the other. Hence when the transfer is effected the migrant may " succeed " extraordinarily well in its new home. If it is a crop plant it will displace from cultivation some of the kinds already growing there, and perhaps change the whole character of the agriculture. The introduction of the potato into Britain is a case in point. If, however, the migrant is a weed the result may be disastrous. The introduction of prickly pear from America into Australia provides a spectacular example which will be discussed later.

The second concept which may be emphasized is that of plants competing for space in which to develop.

Plant Competition

This latter idea of competition amongst plants for living space and survival strikes a dominant note in agriculture. " Successful " plants of use to man, particularly those which accumulate large reserves of food, tend to be used as crops. Those not of use are often weeds. Successful food production turns largely on manipulating and maintaining as far as is practicable an environment so as to favour the desired crop plants and depress natural but unwanted competitiors. Many examples of this will be discussed in a later chapter.

If the general concept of organic evolution be accepted as a long process of trial and error—living things producing new types, the environment eliminating those not fitted for it and preserving those which are—it now falls to see briefly something of the higher plant's body, and how it has come to be as it is.

The Land Plant

It is believed that plant life originated in the water. A major step was taken when the early aquatic types varied in such a way as to produce a body capable of surviving on land. The move on to land demanded firstly the production of an outer covering or skin to prevent desiccation of the living protoplasm. Secondly, a compromise had to be struck between a demand for the exposure of a large surface to light, and the necessity for such strength of body as would permit the plant to resist gravity and other deforming forces which had been "cushioned off" while the plant still floated in water. The first land plants must have been small and remained close to the ground like the liverworts and mosses we see to-day. (Plate 1)

When the soil surface became fully carpeted, any plant there which could grow upwards against gravity would obtain most light and its lowly contemporaries would be shaded. The upward growing habit confers great advantage in the competition for light. The adoption of this posture, however, brought new problems. Water absorption still occurred at or below ground level, hence a system of conduction became essential to connect the organ of absorption with the aerial parts which were losing water.

The body of the present-day higher plant, then, bears all the marks of the struggle for light, the need for protection from desiccation, and the development of such mechanical strength as will connect and hold together its various specialized parts.

The Form of the Plant Body

Essentially all higher plants consist of a main axis like a central back-bone and other parts laterally. Typically this axis consists of a portion in the soil, the root, and a portion in the air, the shoot. The axis is fully strengthened, and internally possesses parts for rapid conduction of various materials from one part to another.

There are very many plants which conform to this description. The great group of ferns and their allies do, but only a few of them enter into agricultural practice, and these as weeds. It is with the specialized land plants which have evolved still further to produce flowers and seeds that agriculture is chiefly concerned.

The seed-producing plants are the highest product of evolution in the vegetable kingdom. Those important to the farmer protect the seed inside a fruit, and are called the angiosperms. Amongst these a great diversity of form is exhibited.

Monocotyledons and Dicotyledons

In order to facilitate study a special " standard type " must first be defined.

This is done, first, by reference to the seed. A seed may be regarded as an embryo plant having an embryonical axis with either only one or only two embryonical leaves. These seed leaves are known as cotyledons. From this the higher flowering plants are divided into those with one cotyledon, the monocotyledons, and those with two, the dicotyledons.

When the members of these two classes diverged in this way from each other early in their evolution, characteristics of the adult body diverged too. In short, there are two main classes of higher seed-plant, each differing in many ways. At this stage three of these differences seen in the adult plant will serve in recognizing and choosing a dicotyledon for study as a standard type.

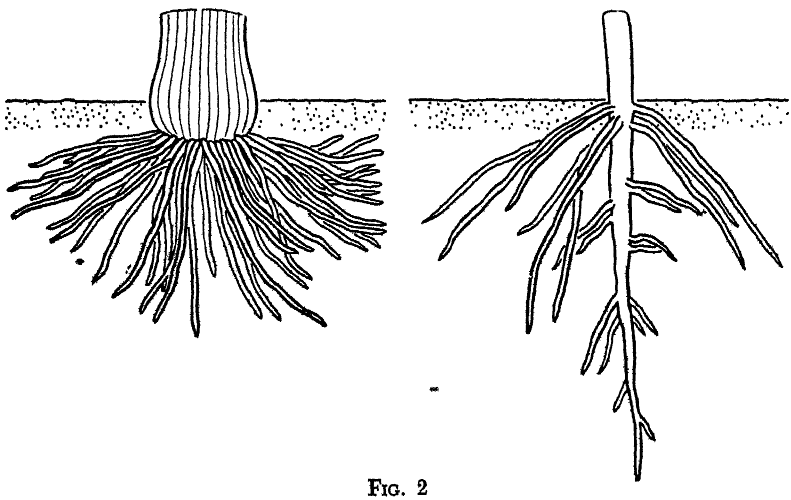


FIG. 2

Left Root of monocotyledon *Right* Root of dicotyledon

The root system of a monocotyledon is fibrous, in a dicotyledon grown from seed it consists of a branched taproot

MONOCOTYLEDONS	DICOTYLEDONS
	Root System
Central axis absent or very short. Many roots, all of equal thickness and length, forming a tuft.	Central main axis present and bearing many side roots or branches —a branched tap-root. No branch as thick as the main central root.
	Leaf
When a leaf is held up between the eye and the light the " skeleton " is seen to be formed from a number of veins all of equal thickness and running in parallel courses.	" Skeleton " made up of one principal main vein and many side branches, the fine venules forming a net-work.
	Flower
The several parts in threes, or multiples of three.	The several parts in fours, or fives, or multiples of these numbers.

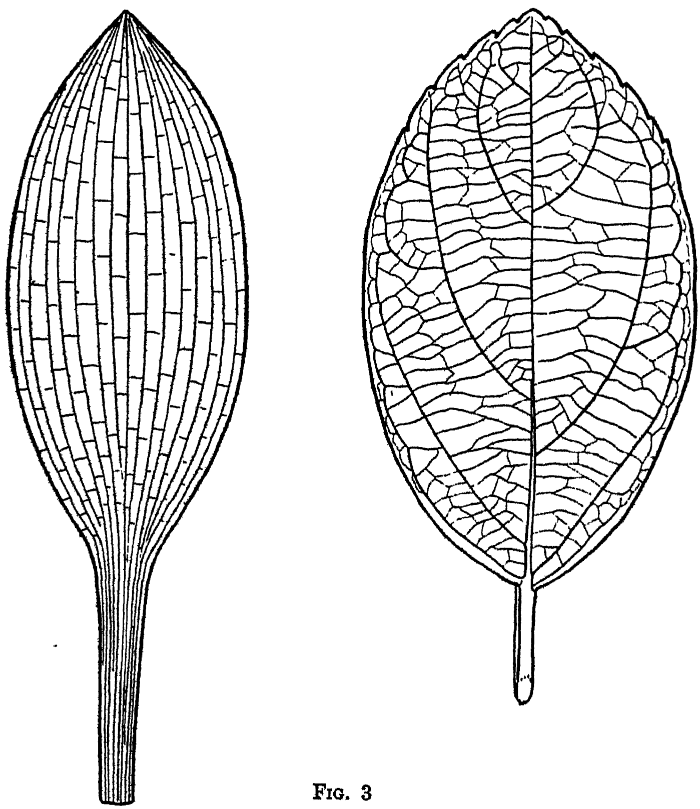


FIG. 3

Leaf venation

Left Monocotyledon

Right Dicotyledon

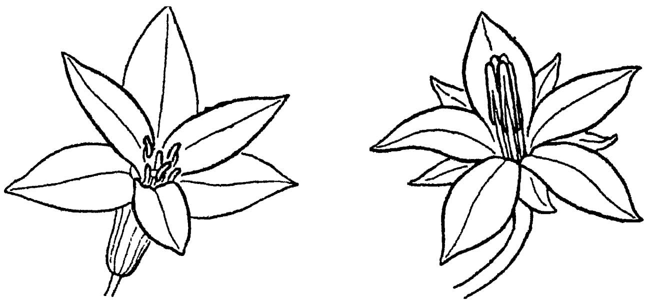


FIG. 4
Flower parts
Left Monocotyledon *Right* Dicotyledon

The plant to which the following chapter will apply is one such as a bean, a wallflower, shepherd's-purse, or any other dicotyledon grown from seed.

A plant of the grass family (including the cereal grains), or a lily or crocus, will not conform to the description, for it is a monocotyledon.

BOOKS FOR FURTHER READING

STRASBURGER, E. *Text-Book of Botany* (a collective work. Trans. by W. H. Lang). This is a general text-book covering the whole subject. (Macmillan & Co., London, 1930)

SKENE, MACGREGOR. *The Biology of Flowering Plants*. (Sedgwick & Jackson, 1938)

Chapter III

MORPHOLOGY AND ANATOMY OF STANDARD TYPES

THE DICOTYLEDON

Morphology may be defined as the study of form or shape. Ordinarily the outward aspect of the plant as a whole is referred to, but it is quite common for the morphology of a particular part or organ to be discussed. Anatomy is the study of internal structure.

Reference Points in Morphology

In both morphology and anatomy the relationships in space of the several parts, one to the other, are important, and so reference points or " landmarks " must be carefully defined as required. The first of these is the plane at which the soil surface meets the plant. This is called the ground level.

The Morphological Axis

Rising above this level and descending below it is the main axis of the plant. This is sometimes called the longitudinal axis or vertical axis, but the best term is morphological axis. In the portion above the ground, at least, it may not be long as, for example, in a red clover plant in winter. It may not be vertical, as in the creeping stem of a procumbent or trailing plant like white clover, or the common pea when it is not supported.

The Root

Typically, the part of the axis below ground consists of the main axis striking down into the deep layers of the soil. Because it " taps " the supplies of water and minerals there it is called the tap-root. It is recognized as a root because all the side or lateral members it bears are identical with it in all respects except perhaps size. This leads to the definition of a root as a plant organ which has as its chief function the absorption of water, and which normally bears no lateral members other than replicas of itself.

Root Branches

When an organ bears a lateral member like itself it is said to branch, and the member is called a branch. Branches arising on the axis itself are primary, or branches of the first order. When a primary branch in its turn forms a subsidiary, this one is called a secondary, or branch of the second order. The primary branches are not all of equal length, thickness, or age. The oldest, thickest, and longest ones come off the axis nearest the surface of the soil, while the youngest, shortest ones arise on the axis some little way behind the tip. When branches are arranged in this way they are said to have arisen in acropetal succession.

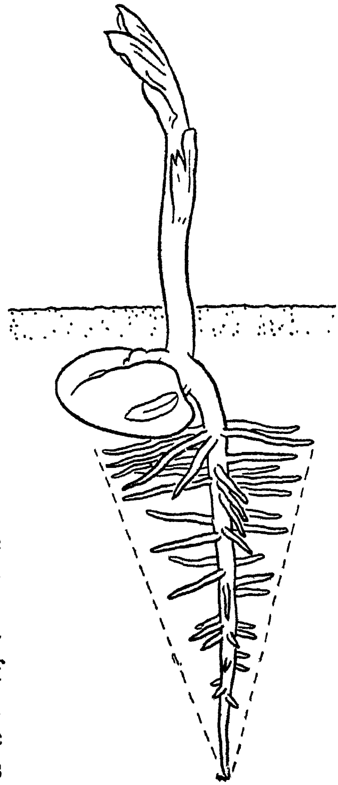


FIG. 5
Roots of dicotyledon plantlet

If lines are imagined connecting the tip of the axis with the tips of the longest branches at each level, they will trace out a cone. The base of the cone will, of course, be towards the surface of the soil and the apex directed downwards in the soil. The morphological base of the root axis is at the centre of the base of this cone, and the morphological apex of the root will be at the point of the cone. The tap root and its branches constitute the root system of the plant.

It will be noticed in this definition and discussion that it has *not* been said that roots are non-green. Roots may become green if exposed to light. Nor has it been said that they are in the soil, for roots can and do occur above the soil surface.

The Stem

At or about the base of the tap-root there is a small transition region, and then above that the axis continues into the main stem. This region of the axis may be short or long, green or non-green, depending on circumstances, but if it is a true stem it

will bear members unlike itself called leaves. This constitutes the primary difference between a stem and a root.

Leaves

Leaves are organs developed from the superficial layers of a stem, and in an order and arrangement typical of the plant which bears them. They do not repeat the shape or internal structure of the stem.

Nodes and Internodes

Where the leaf joins the axis, the stem is slightly thickened like a little knot or node, hence this part is called the node. The bare portion of axis extending between nodes is called the internode. A stem axis then is constructed of alternate nodes and internodes. Closer examination of a node will show that the leaf diverges outwards and subtends an angle with the main axis. This angle is called the axil of the leaf.

In the axil of the leaf the stem bears a bud. Always, a true leaf has a bud in its axil. The leaf may fall off, as from a tree in winter time, but a scar is always left on the surface where it was attached. A node, then, is that point in a stem where a leaf or its scar of attachment subtends a bud.

The Bud

A bud is merely a very young stem in which the axis has not yet elongated ; the internodes are short, and the leaves not fully expanded. The young leaves and delicate axis tip may be protected by an outer layer of leaves modified to scales.

There are two kinds of bud on a stem. Those which terminate stems are called terminal buds, and those which occur in the axil of a leaf are called axillary or lateral buds. Both kinds may be either active (growing) or inactive (dormant). In a perennial, such as a tree which casts its leaves, all buds are dormant during winter. A terminal bud in active growth provides for the elongation of the stem which bears it.

When an axillary bud becomes active it develops into a branch, provides for its elongation, and becomes the terminal of that branch. A terminal bud is sometimes called a " leader."

Many lateral buds normally remain quiescent indefinitely, and indeed after a year or two abort. In the growing of fruit

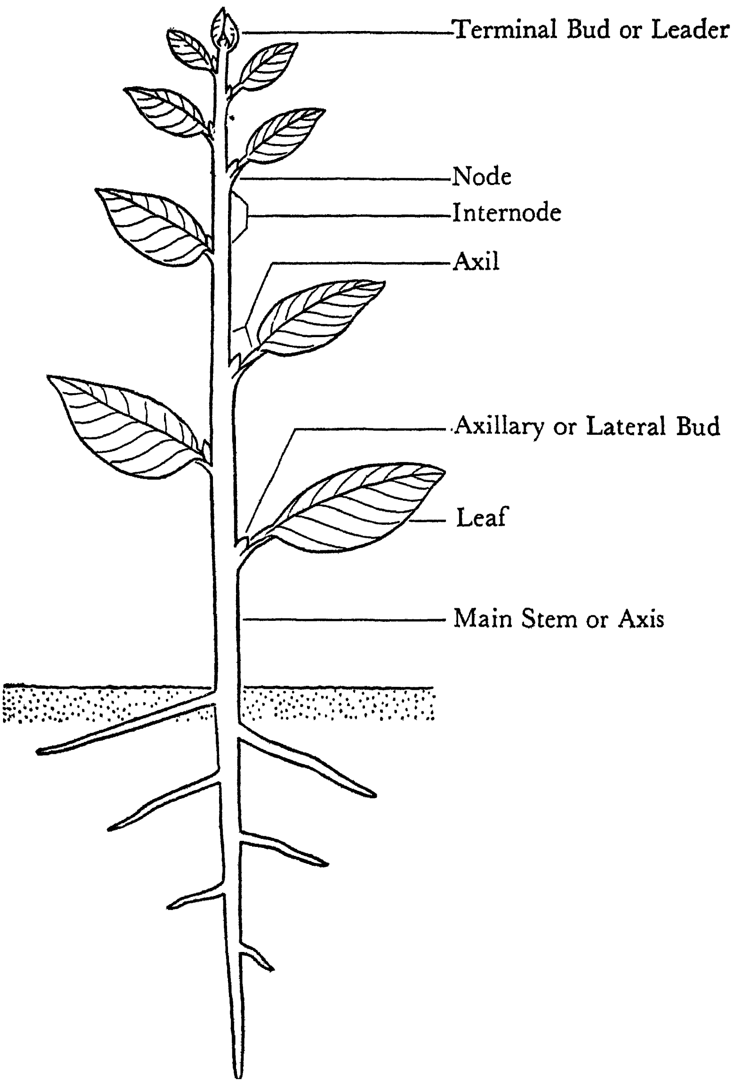


FIG. 6

The parts of the shoot system

and other trees, persistent and dormant buds at the base of the trunks may become active for no apparent reason. The branches so produced are usually useless and called suckers.

In many plants it is normal for the terminal bud to provide for elongation of the branch during part of the season only;

after this it forms flowers or other parts. It ceases to "lead." This has the same effect as loss of the terminal by accident or pruning. The result is, the lateral bud first below soon becomes active, straightens up more or less into line with the original axis and takes the lead.

In some plants, as, for example, many of the fruit trees, some of the branches are specially reserved for flower and fruit production. The leader of such a branch adds very little in each year, while the lateral buds form flowers. After a few years this

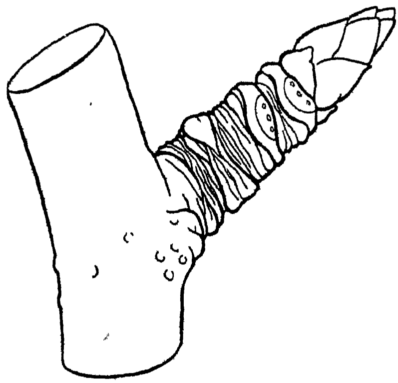


FIG. 7
A fruiting spur in winter

fruiting spur, as it is called, is still quite short, and has its surface covered with scars where leaves and fruit stalks have become detached.

THE ARRANGEMENT OF PARTS ON THE SHOOT

The stem axis, its buds, branches, and leaves, constitute the shoot system of the plant. The morphological base of the shoot system is at its junction with the root axis. It is clear that the youngest leaves, and therefore youngest buds or branches, are nearest the apex of the axis. They arise in acropetal succession. In addition to this leaf arrangement along the axis, an arrangement round its cylinder can be seen.

Phyllotaxy

In many plants, when the points of insertion of the leaves are connected by an imaginary line, it traces out a helix or spiral like a winding stair. This is called a spiral arrangement. If, in

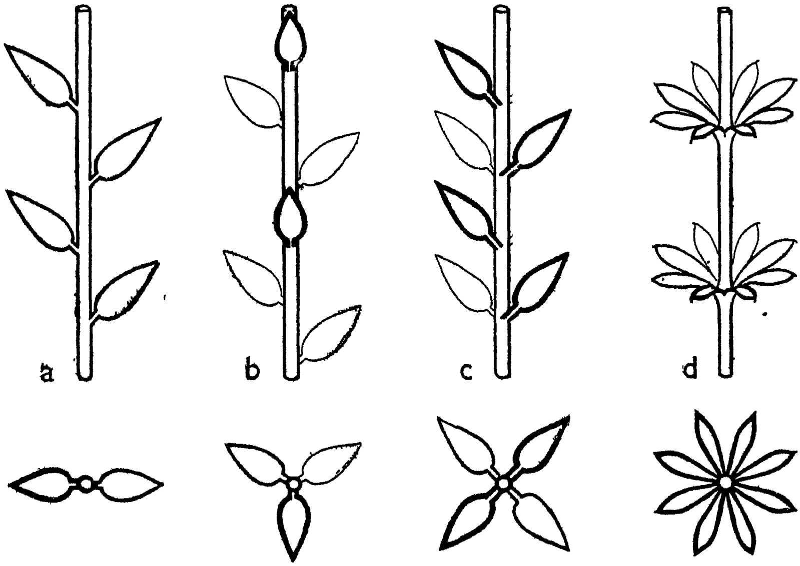


FIG. 8

Leaf arrangement

(*a*) Alternate in two rows (*b*) Alternate in three rows
(*c*) In pairs opposite (*d*) Whorled

The " ground plan " of each is also shown

passing from the base of one leaf to the base of the next one above it, the line passes round one half of the stem, the arrangement or phyllotaxis is said to be a half. The leaves will be alternate in two rows up the stem. If the line travels only one-third of the way round the stem in passing from one leaf to the next above phyllotaxis is one-third, and the leaves will be in three rows. The fraction found for any one kind of plant is definite and typical of it. Phyllotaxy differs as between different kinds of plant.

In some plants the phyllotaxis is not spiral, for more than one leaf comes off at one level. If two are at one node they are said to be in pairs. If successive pairs are inserted on diameters of the axis cylinder which are perpendicular to each other, the leaves are said to be opposite and decussate. If more than two leaves come off at one level they are said to be in whorls. A knowledge of phyllotaxy is important for two reasons. First, it indicates the way in which branching will take place and a tree may be " shaped " by pruning. Second, it assists in identifying plants at certain times, as, for example, woody twigs in winter.

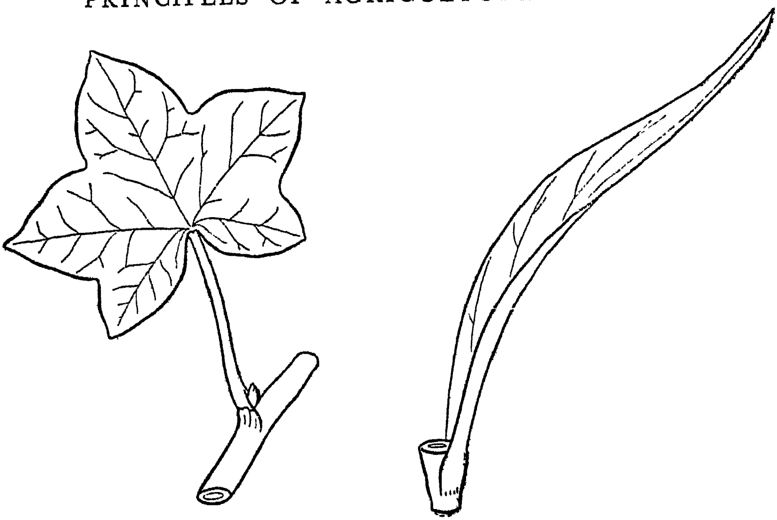


FIG. 9

Left A petiolate leaf *Right* A sessile leaf

THE LEAF

The primary function of a leaf is the absorption of light in food making, and therefore it is desirable that one individual should not overshadow another. The ideal is that leaves should " fit into " each other and form a mosaic. When the flat leaf is attached directly to the stem this ideal is difficult to achieve. Many leaves are therefore formed of two parts, a flat blade or lamina carried out from the stem on a leaf-stalk or petiole. Leaves of this type are described as *petiolate*. On the other hand, a leaf which consists of a blade or lamina only, attached directly to the stem, is said to be *sessile*. Methods of branching, arrangements of leaves, torsion of petioles, modification of lamina shape, etc., all help to prevent overshadowing, and go towards the production of an efficient light trap.

Leaf Shape

Leaf shape may assist in this regard, and varies considerably. In some plants the lamina is a more or less complete oval with the edge quite entire. This is the simple leaf which in somewhat more advanced forms becomes incut. In the most advanced forms the incuts extend right to the centre of the blade, so that the lamina is divided into separate portions. Each separate portion of a divided lamina is a leaflet. A leaf composed of leaflets is said to be compound. There is no bud at the base of a leaflet.

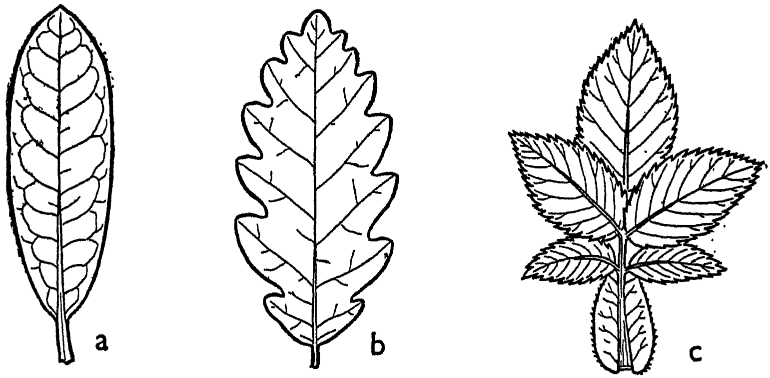


FIG. 10
Leaf shape—one main vein
(*a*) simple (*b*) lobed (*c*) compound
Note in (*c*) the petiole is expanded to form two small "wings" called stipules

SUMMARY OF THE MORPHOLOGICAL REGIONS OF THE PLANT

The picture, then, is of two regions or systems in the plant. There is the root system branching and rebranching, usually underground, exploring the largest volume of soil compatible with the habit of the plant. In the air is the shoot system, branching and extending so that, by its leaves, it may hold up to the light the maximum surface compatible with the existence of the plant.

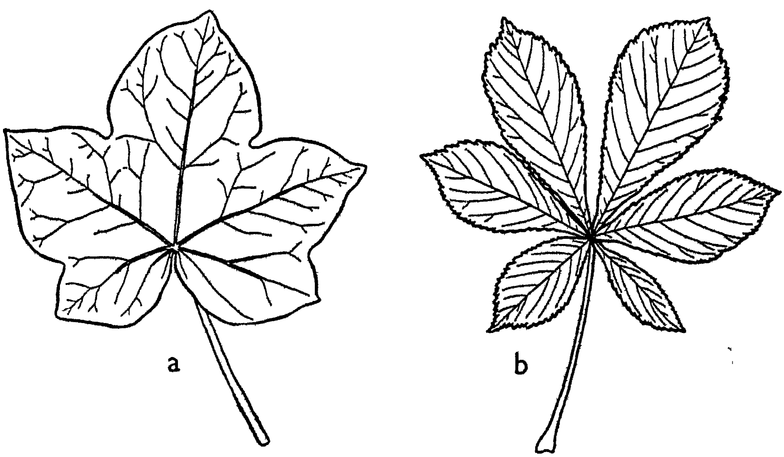


FIG. 11
Leaf shape—more than one main vein
(*a*) simple lobed (*b*) compound

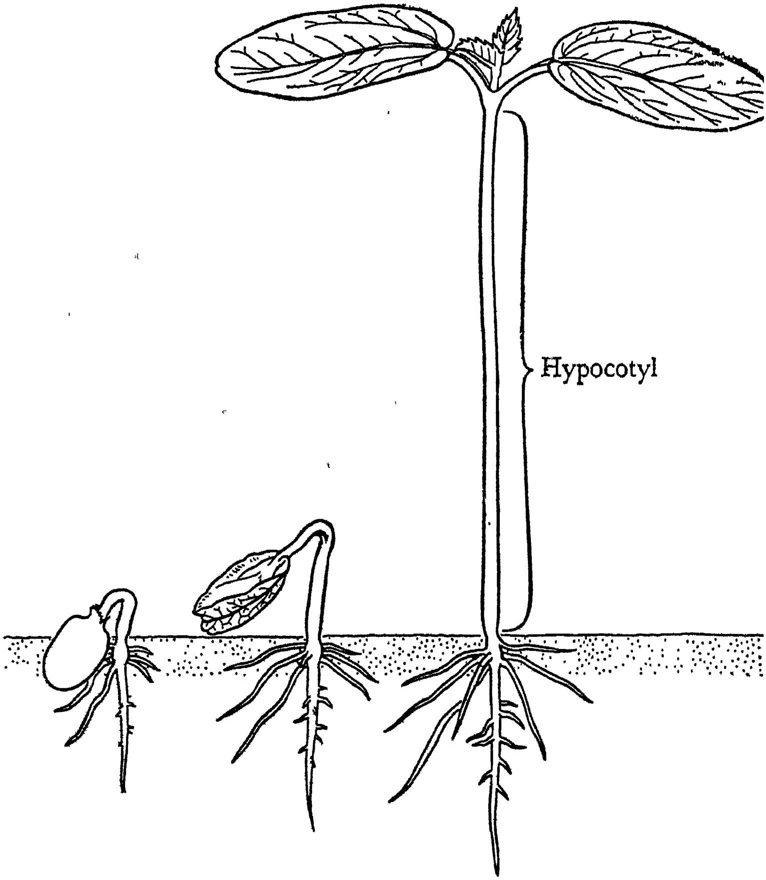


FIG. 12

Epigeal germination of Castor Oil plant

The cotyledons act as suctorial organs absorbing the endosperm. They are carried above the soil and expand as green leaves

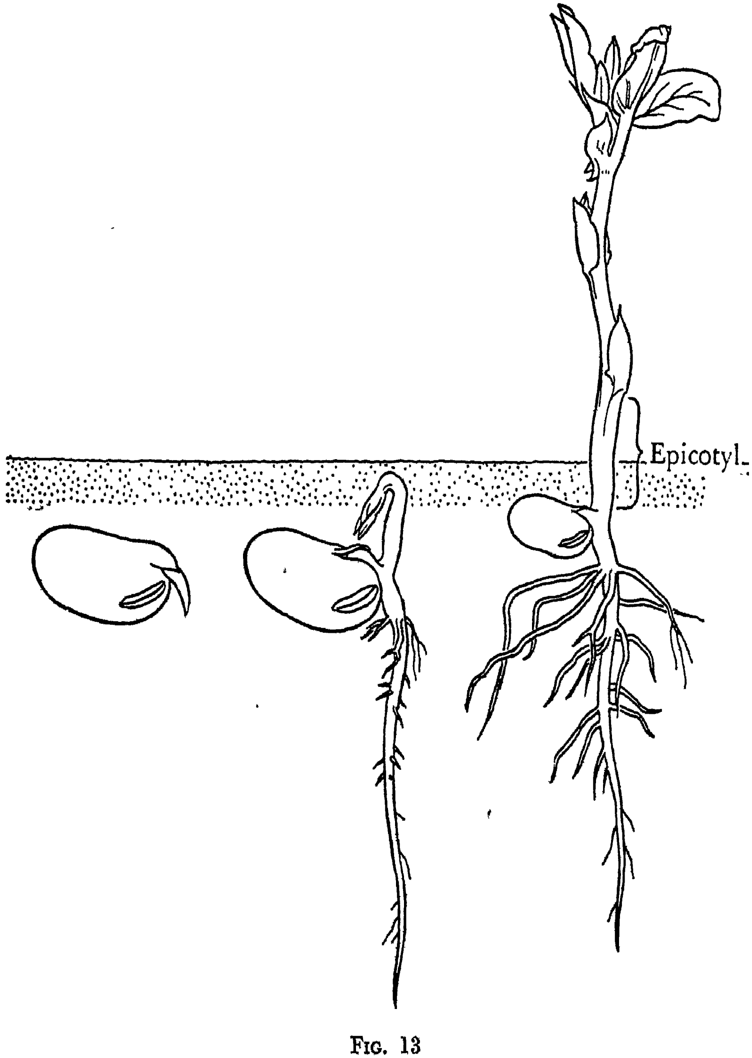


FIG. 13

Hypogeal germination of Broad Bean plant

The cotyledons full of food remain below ground and the young plant draws nourishment from them

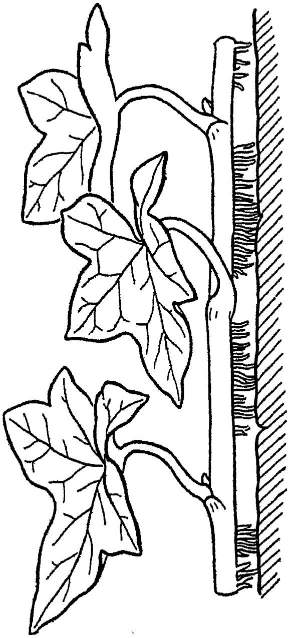


FIG. 14
Adventitious roots
Aerial roots rising on the stem in ivy

Adventitious Organs

In connection with roots, stems, and buds the word adventitious is often used. This indicates that the member in question has arisen in a peculiar place. For example, if a gardener cuts off an appropriate piece of stem and places the cut end in soil, roots may develop in the region of the wound. These roots arising from a stem are adventitious roots. Similarly, some roots if cut off and specially treated will produce buds. These are adventitious buds. Adventitious roots often develop naturally; as, for example, those commonly seen on the stem of ivy as it clings to a wall.

SEEDLING MORPHOLOGY

The formation of all these various parts in each generation proceeds from the development of the small embryonic plantlet seen in the dry seed. This little structure shown in Fig. 69 (page 166) consists of a short axis which has at its apex an embryonic terminal bud (the *plumule*) and at the other end an embryonic root-tip (the *radicle*). At a point between these two extremes the cotyledons are attached or inserted. The region of axis between the insertion of the cotyledons and the plumule is called the *epicotyl*, while that portion below the cotyledons is the *hypocotyl*.

During the process of germination and subsequent growth either the hypocotyl or the epicotyl lengthens, but not both. If the hypocotyl lengthens the cotyledons are carried up above the surface of the soil and germination is described as *epigeal*. Conversely, if the epicotyl lengthens the plumule alone will come above the soil level and the cotyledons will remain buried in the soil. When this happens and the cotyledons remain in the earth germination is described as *hypogeal*.

These two cases may be summarized:

Portion of Axis which Lengthens	Type of Germination
Epicotyl	Epigeal
Hypocotyl	Hypogeal

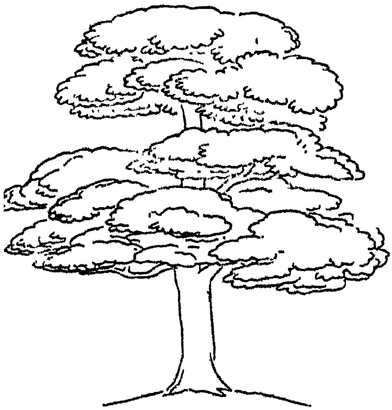
In the more nearly adult plant the two regions may be recognized for, roughly, the insertion of the first leaf above the cotyledons marks the top limit of the epicotyl, while the origin of the first branch root marks the lower limit of the hypocotyl.

Anatomy

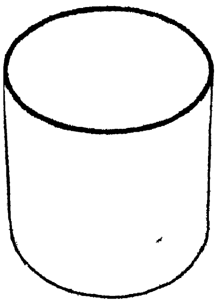
Reference Points, Lines, and Planes

Having defined the various regions of the plant, it now falls to see something of their internal structure or anatomy. Once again it will be appropriate to lay down reference points, lines, and planes. As we have seen, a root axis plus shoot axis forms a cylindrical structure, the growing points at the distal ends and the junction of one with the other at the proximal ends. The line joining the two apices is the morphological axis. Any plane or section at right angles to this line is called a transverse plane or transverse section. Any section parallel to the morphological axis is a longitudinal section. There are two possible longitudinal sections: one which cuts longitudinally down on any radius of the transverse section. This is known as a longitudinal-radial section. In the other longitudinal section the plane of the cut is parallel to the morphological axis and down any line tangential to the circumference of the transverse section. This is the longitudinal-tangential section. The contractions usually used to denote these three sections are T.S., L.R.S., and L.T.S.

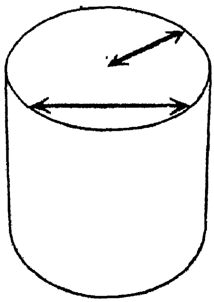
In considering a leaf a little trouble may arise. The part of the leaf proximal to (that is, nearest to) the stem is the base, and the part farthest away (distal) is the apex. The line connecting base with apex is the morphological axis. Any plane cutting across this line at right angles is a transverse section. The blade of the leaf is not often radially symmetrical about this axis, but is typically flat with upper and lower surfaces. Any plane which cuts through the leaf perpendicular to the surfaces is a



The axis is a cylinder

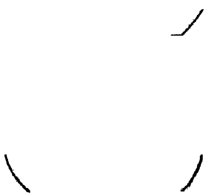


T.S. exposed



The radius and tangent

L.R.S. exposed



L.T.S. exposed

T.S., L.T.S., two L.R.S.'s exposed

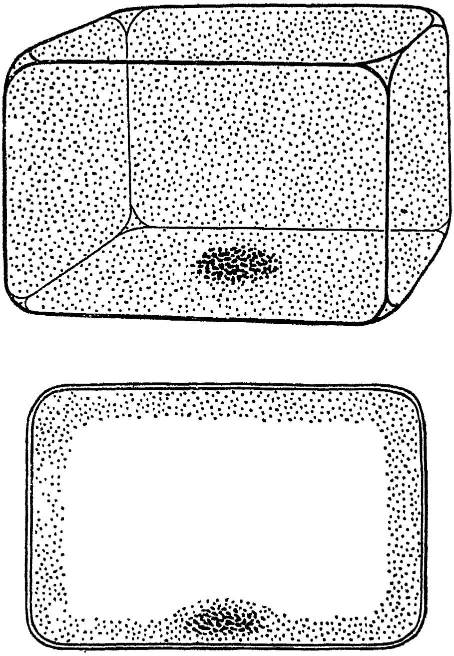
FIG. 15

The sections of a cylindrical organ

FIG. 16
The plant cell

(*a*) In perspective. A box of cellulose lined inside with protoplasm in which a nucleus is immersed

a



(*b*) Seen in section. Note the wall, protoplast, and denser nucleus

b

vertical section. This term may be usefully applied to a plane perpendicular to the surface in any flat organ.

THE CELL

The anatomy of a plant is studied by observing thin slices (sections) of the various parts under some degree of magnification. Observation is often assisted by staining the preparation with appropriate dyes. When a section is examined it is seen that the higher plant is made up of a large number of small units or cells. All plants are cellular in structure. Each cell is a discrete unit, and when alive consists of a portion of living protoplasm with a nucleus immersed in it. Physically, protoplasm is rather like thin jelly and almost colourless. Chemically, it is formed of a mixture of proteins. The nucleus is rather more viscous and chemically is more complex. In the plant practically all cells are enclosed within a non-living wall. The plant cell may be pictured as a one-compartment box filled or lined with living contents.

The Multicellular Plant

There is no doubt that the very primitive plants were very small and consisted of one cell only. Forms of these unicellular types can be seen to-day, usually living in water. Such a self-contained unit is not capable of elaborate organization. If, however, in early evolution a group of these unicellular organisms remained stuck together and did not separate, each could aid the other slightly. This probably happened and a " colony " of individuals developed. Later in evolution, different members of the colony took on special duties or functions, each undertaking a specialized part of the whole work of the group ; a degree of organization appeared, and a form of multicellular organism was created.

How the Many Cells are Produced

All highly evolved living things during their life repeat some of the evolutionary history of their race, and this is seen in plants. Each individual starts life as a single cell. This divides into two. These two each divide, and so give four cells. In time this process of division provides a group of cells all apparently alike. The greater part of the group alter the nature of their contents, their shape, and the nature of their walls, so as to become specialized for special functions. Each and every cell of the very many making up the plant body starts off in the embryonical condition as a result of division of a pre-existing cell.

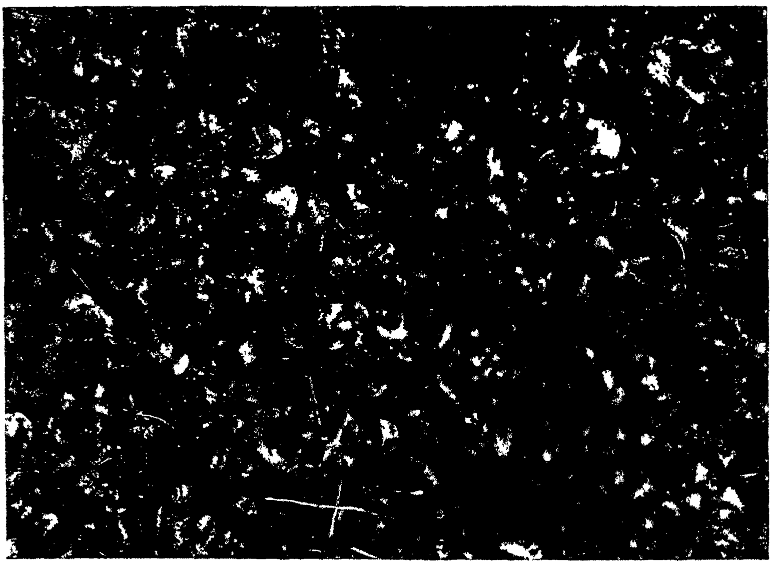
The process of division of body cells is seen when a small portion of an actively growing part, such as a root tip, is killed and " fixed." Fixation is done by immersing the tissue in some chemical which quickly penetrates the tissue, and by its action " freezes," as it were, the individual cells in the state they were in life. Sections made of such a tissue are then stained with appropriate dyes.

Division to Form Cells of the Body: Mitosis

The nuclei take the dominant part in division and different cells in the section will show different stages of the process. The earliest evidence that a division is about to take place appears when in a cell the amorphous mass of the nucleus seems to have condensed into a long tangled thread, more deeply stained than the surrounding protoplasm. Cells in a later stage will be seen where this thread is thickened and has attracted the dye even more avidly.

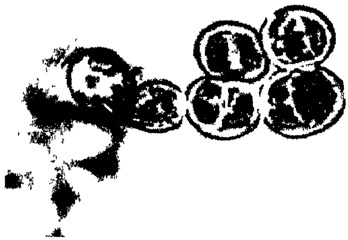
PLATE 1 LIFE ORIGINATED IN WATER

An early step in the move from the water to the dry land

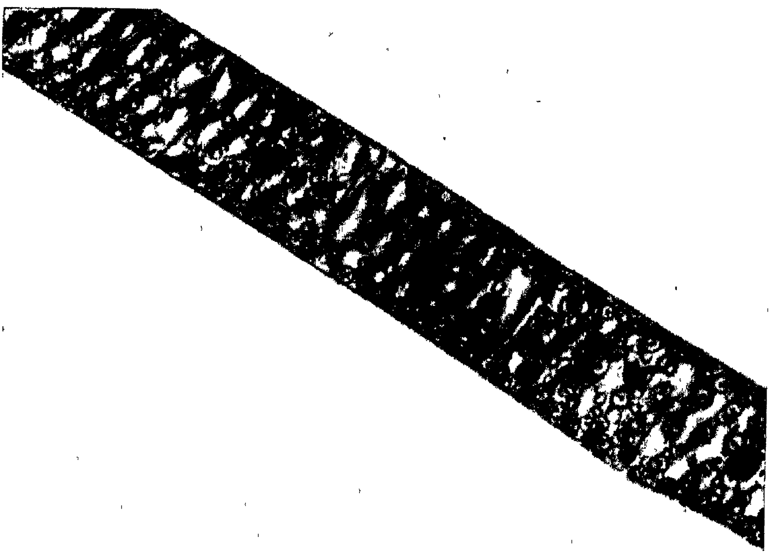


The first land plants must have kept close to the soil. They had little mechanical strength and dried out easily

PLATE 2 SIMPLE GREEN PLANTS



A plant capable of normal life as a single cell tends to form a colony. Each cell is green and fully functional



A simple multicellular plant. Note the large nucleus (lying centrally) and the other living contents filling each cell

FIG. 17

MITOSIS:

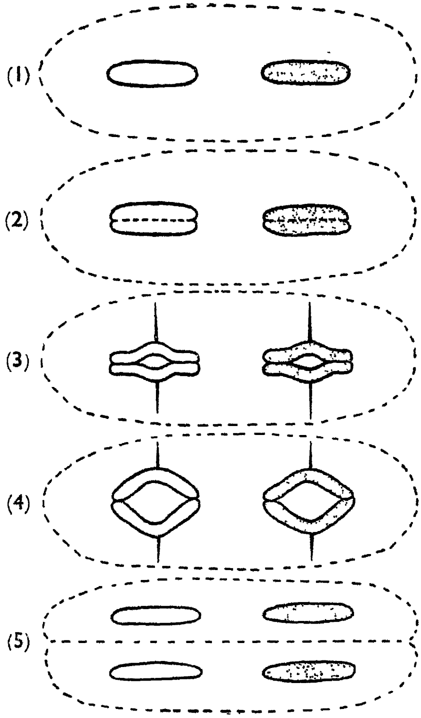
What happens to one of the pairs of chromosomes

(1) The cell in the earliest stage

(2) The chromosomes show the start of the split

(3) & (4) The split halves are pulled apart

(5) Two cells are formed, both equal and equivalent to the original



Next, the nuclear thread breaks up into short rod- or dot-like bodies. Because of their ability to stain deeply with appropriate dyes in this way, those " coloured bodies " are called *chromosomes.*

Different chromosomes differ in length or perhaps in shape, but very soon it will be seen that in each nucleus there are two of each particular size or shape. The chromosomes in the nucleus of a body cell are paired. The members of such an identical pair are homologues and constitute a homologous pair. In the usual case, no matter where or when actively dividing cells in the body of any given species are examined, the set of chromosomes is identical as to number of pairs and the shape of the individuals composing each pair. The number, size, and form of the chromosomes in the set is constant for the species.

As the process of division proceeds, the chromosomes come to congregate on a plane at the " equator " of the nucleus—the equatorial plate. Once the chromosomes are arranged on this plane or imaginary plate, each one is seen to separate down its long axis into two exactly equal halves. The pairs have duplicated.

Lines of fibre-like structures now radiate out from what may be referred to as the poles of the cell. Each fibre extending out from each of the poles to the equatorial plate attaches itself to a half-chromosome. One fibre from one pole goes to one half-chromosome, while a fibre from the opposite pole goes to the other half of the same chromosome. The polar fibres now appear to contract, each pulling one half-chromosome towards the pole. The half-chromosomes part company, one to one pole and the other to the opposite pole. Each lot of half chromosomes in this way congregates at or near the pole of the original or " mother " cell. The two congregations of half-chromosomes each includes a specimen half of every chromosome in the original " mother " nucleus. So are formed two " daughter nuclei " identical in chromosome content and exactly similar to the " mother " nucleus.

The chromosomes in these derived or " daughter " nuclei now lose their sharp outline and shape. A process of dissolution sets in to form a jelly-like blob similar to that seen in the original nucleus. As the chromosomes lose their identity a cross wall forms in the equatorial plane, and cuts the protoplasm originally present into two equal portions. This first thin common wall is called the middle lamella. Two cells with protoplasm and a nucleus are constituted. This is *mitosis* or somatic division, whereby a cell of the body or *soma* divides to form two cells. These are qualitatively identical, and each exactly similar to the cell from which it was derived.

The two daughter cells formed from such a mitotic division are then supplied with food from the main body of the plant and soon increase quantitatively to the size of the original " mother " cell. They are then ready either to divide in their turn or alternatively to modify into permanent elements of the plant body. In a growing point it is only the cells nearest the tip which divide ; those towards the rear modify.

Once a cell has modified to any extent it becomes incapable of division. In certain cases, cells only very slightly modified, if properly stimulated, become young again and recover this ability.

Aberrant Mitosis : Heteroploidy

Very occasionally the processes of cell-division are interrupted or partially disorganized, so that the two derived nuclei do not receive exactly equal halves of the chromosome set seen in the

original nucleus. The cell-wall which normally parts the daughter nuclei may be omitted, and a bi-nucleate giant cell is produced. Or one or more chromosomes of a set may be diverted to the wrong pole and two nuclei of different constitution result. One of these will be plus one, or more, chromosomes, while the other will be minus the same number. These two forms of aberrant division may be regarded as extremes, and various intermediate degrees of the abnormal may occur. Any nucleus which shows an aberrant number of chromosomes is said to be *heteroploid.*

If a heteroploid nucleus is not too extremely aberrant it is capable of division, and the cells of a tissue derived from it are also heteroploid. Plants with heteroploid nuclei may differ morphologically or physiologically from the parent, and be of more value in agriculture. This "useful" aspect of the phenomena will be dealt with in Section Four.

Induction of Heteroploidy

Heteroploidy may be induced in three different ways. In nature by extremes of some external factor, such as temperature. In culture when a plant is mutilated very considerably as by drastic disbudding, cells of the callus tissue which forms on the wounds may organize buds, and some of these may be heteroploid. Again, certain chemicals, for example colchicine, when applied to the plant in very high dilution, interfere with cell division. If the concentration used is too low no effect is produced, if too high the plant dies. Plants differ quite considerably in their sensitivity to the different drugs and their concentration. There is a concentration of each drug for each plant which produces just such an upset of division as will not cause death.

The differences in sensitivity between the different plants are further exploited, not to form new plants, but to kill some and leave others unaffected. Some selective weed killers are chemicals of this class, and these will be further discussed in Section Three.

Tissue Formation

Any group of cells all having the same form and engaged in the same function is called a tissue. A group of cells engaged in mitotic division is called a meristematic tissue, or briefly a meristem. Obviously a meristem may be looked for in any part

where growth is active. Meristematic tissue is easily recognized, for the cells are uniform in shape, being somewhat brick-like, have thin walls of pure cellulose, and are packed tightly together. There are no spaces between cells, and inside the walls the cavity or lumen is quite full of protoplasm with the nucleus lying in the centre. A meristem is derived from a previously existing meristem. Those seen at the tips of the tap-root and primary shoot, derived as they are from the embryo, are primary meristems. Where slightly modified cells in older parts of the plant reassume ability to divide, the actively dividing cells so produced constitute a secondary meristem.

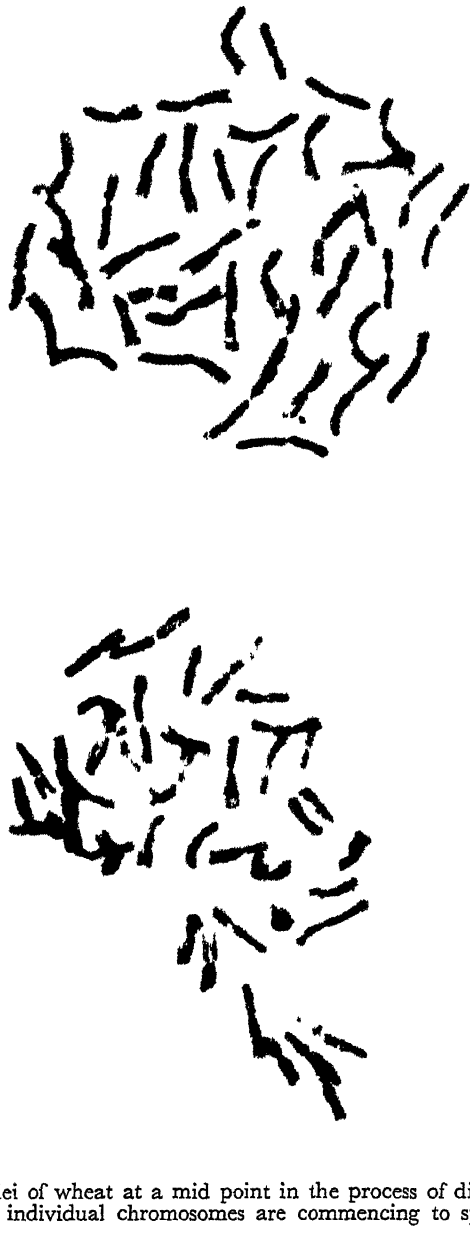
Cell Modification : Simple Enlargement and Intercellular Space Formation

From the quite unmodified simple cell produced by mitotic division come all the various kinds of cell composing the different tissues of the plant. Each particular cell-kind is known as a tissue element. In the simplest form of modification, the individual cells produced in the meristem lose their angular shape and round off. By degrees they each become larger and somewhat spherical. One result of this change in shape is that little spaces appear in the tissue between individual cells, very much as they do between individuals in a heap of potatoes or tennis balls. These are the intercellular spaces. Each intercellular space is connected with its neighbours. The spaces between cells form a continuous network filled with air. Oxygen or any other gas can therefore pass through this ramifying system of passageways to reach any and every cell. The cells too form a complementary network, for every one is in contact at different points with its three or four immediate neighbours. Liquids and dissolved substances can pass through the walls from cell to cell at the points of contact.

Vacuolisation

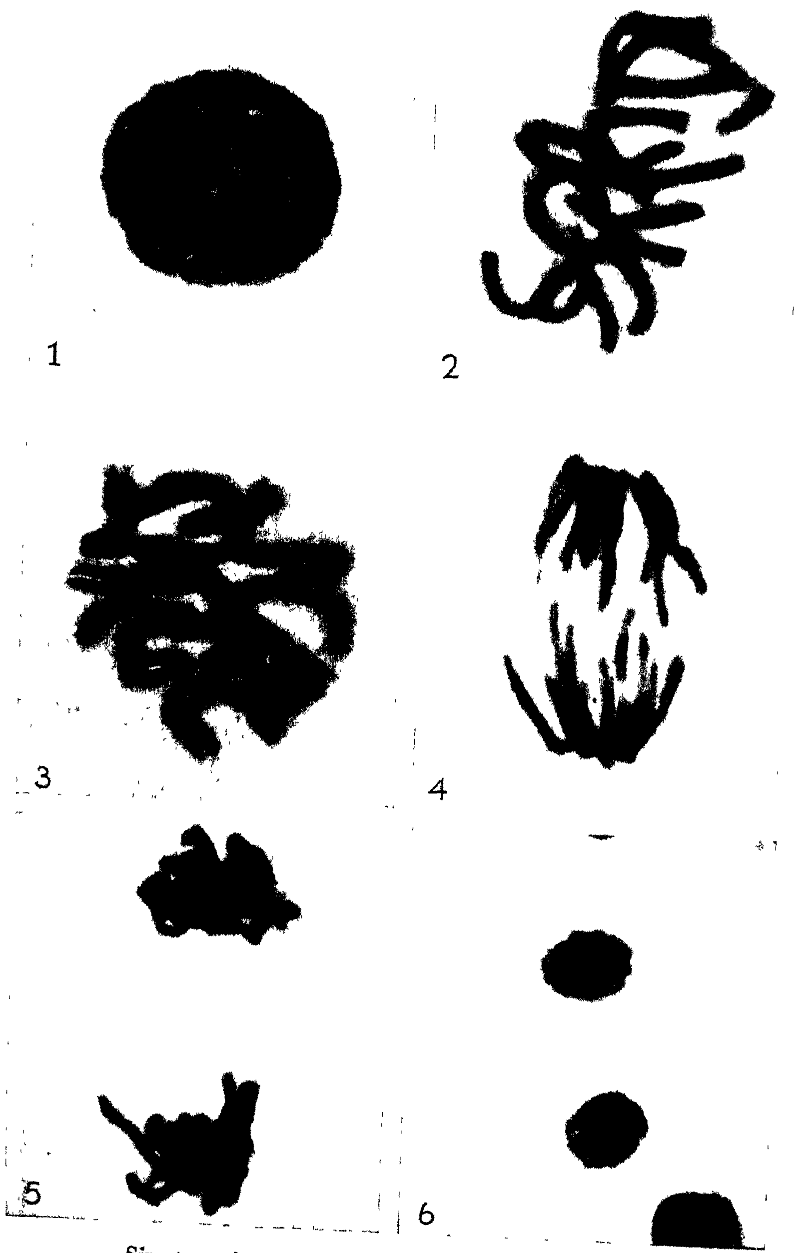
While each cell is assuming the spherical shape it expands. This increased volume is due to watery fluid accumulating in the protoplasm in droplets. Each of these drops enlarges. Finally, when the cell has reached its full size, the individual drops run together in the centre of the cell, forming one big drop called the vacuole.

PLATE 3 CHROMOSOMES



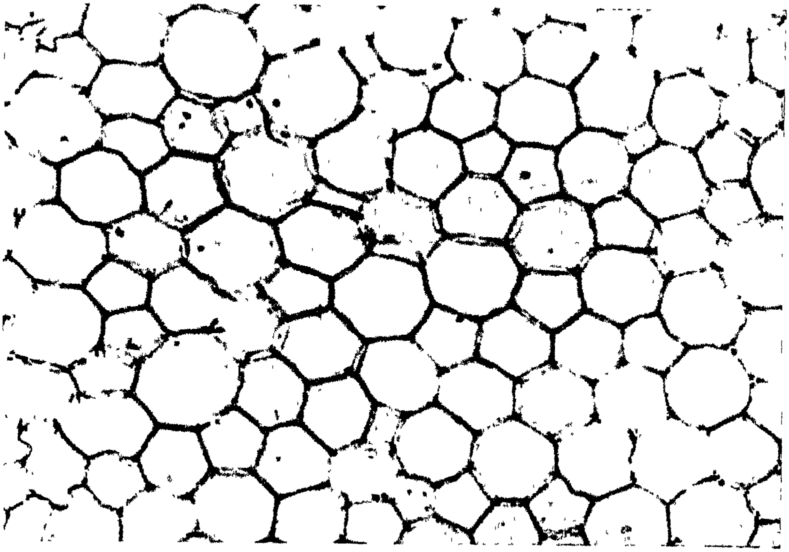
Two nuclei of wheat at a mid point in the process of dividing.
The individual chromosomes are commencing to split

PLATE 4 MITOSIS

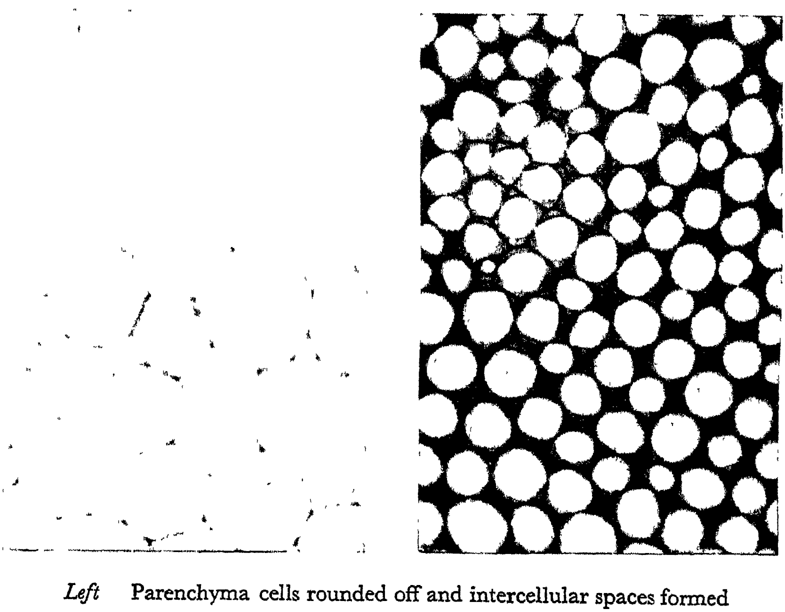


Six stages in the process of division in a body cell

PLATE 5 CELL MODIFICATION

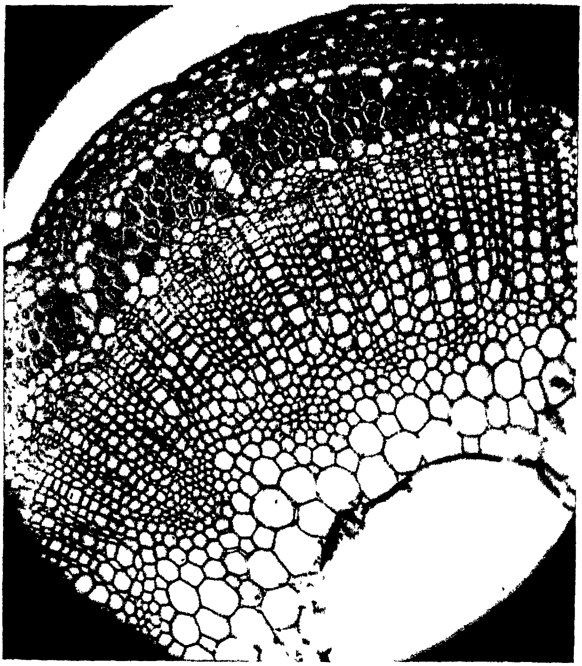


Newly formed parenchyma. Each cell is thin-walled: there are no intercellular spaces

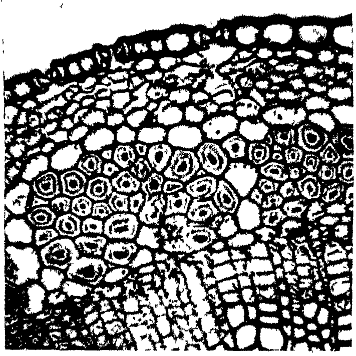


Left Parenchyma cells rounded off and intercellular spaces formed
Right Collenchyma as seen in T.S. of a stem

PLATE 6 PROSENCHYMA OF FLAX



T.S. stem to show prosenchyma massed towards the periphery



Prosenchyma larger magnification than that above

Prosenchyma highly magnified

Note the very small cell cavity due to extreme thickening of the wall

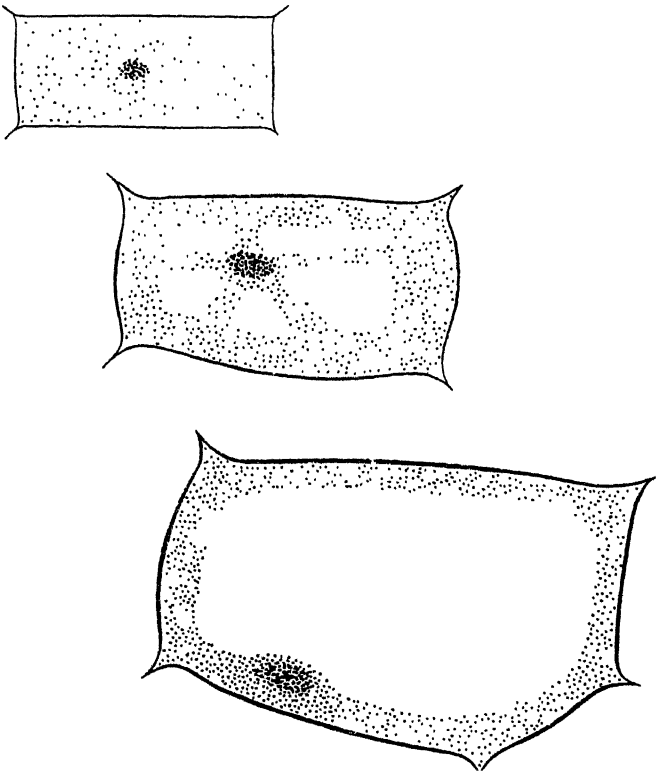


FIG. 18
Progressive steps in vacuolisation

Parenchyma

The final appearance of such a cell is that of a spherical wall lined on its inner surface by a layer of protoplasm in which is immersed the nucleus. The main volume of the cell is filled with the watery sap of the vacuole. A tissue composed of such elements is called parenchyma, and the cells are described as parenchymatous.

When parenchyma is used for storage, starch-grains, oil-droplets, crystals of inorganic compounds, and other solid non-living inclusions may be deposited in the cells. Soluble material remains in solution in the cell-sap.

Further modification of parenchyma affects the walls rather than the contents of the cell. The wall may alter considerably in

shape or may be altered chemically, while the protoplasm and nucleus either remain unchanged or are taken out of the cell altogether.

Cell Wall Modification

The various more spectacular cell modifications leading to formation of special tissue elements may now be described. The simplest of these consists in the thickening of the cell wall with more cellulose. Usually cellulose is spread evenly over the wall surface, apart from little thin areas left where cells abut. These thin spots in a thickened common wall are known as pits, and the wall is described as pitted. The pits provide for seepage of water and other material from cell to cell.

Collenchyma

In peculiar cases the thickening is not deposited on the common wall between cells, but is concentrated on those parts where cells abut on intercellular spaces. While this particular kind of thickening is going on the cells concerned usually change shape and elongate in a line parallel to the long axis of the organ they occur in. A cell so produced is seen in transverse section as roundish in outline with thickenening " at the corners " ; in longitudinal section it appears more like a fluted column. Such a cell, or a tissue composed of a number like it, is called collenchyma and described as collenchymatous. Obviously, thickening of the wall increases mechanical strength, and the collenchymatous type gives greatest strength in a longitudinal direction—that is, " up-and-down " a stem or root.

Prosenchyma and Sclerenchyma

Where greater strength is required than that provided by collenchyma, the elongation of each cell is carried still further. This in the extreme case provides cells many times longer than broad. The individual cells slip one over the other, so that each presents a great portion of its surface to its neighbours. Wall thickening always accompanies such elongation, and this may be carried so far as nearly to fill up the whole interior of the cell with wall. When extreme thickening of this type occurs the living contents of the cell disappear.

A tissue made up of cells many times longer than broad, each with a thick wall and devoid of living contents, is described as prosenchymatous. The prosenchyma cells are often called fibres. The beautiful fibres got from the stem of the linen plant (flax) are of this nature. Linen fibres are long, hair-like cells with walls of nearly pure cellulose, so thick as almost to fill the cell cavity.

Many other plants produce equally long fibres, but in them the walls are considerably modified by the addition of some material other than cellulose. A substance called lignin is commonly used by the plant for this purpose. A tissue made up of long fibrous elements, whose thick walls are hardened by lignification, is termed sclerenchyma.

Possession of a sclerenchymatous tissue confers great strength on an organ, for not only are the individual fibres very strong, but owing to their great length each one overlaps its neighbours for quite a long distance, so that they adhere together very powerfully.

All the purely mechanical tissues of the plant are made up, wholly or in part, of one or other or some combination of these four elements.

Elements for Water Conduction: Vessels

When specialized function has to be provided for, more elaborate modifications have to be made. For example, water passes but slowly from one cell to another, and some method of fast conduction is required. Where conduction or mass flow of liquids is to be engaged in "pipes" must be constructed. To do this a line of cells one above the other extending from the growing point of the root to the growing point of the shoot is involved. Each cell elongates in a line parallel with the morphological axis of the organ. Then the cross walls (*i.e.* walls transverse to the axis) are dissolved out and the living contents absorbed. This gives a long empty tube running from the distal end of the root right up through the shoot.

Vessel Thickening

Like any other pipe whose walls are soft, they would be liable to burst under pressure or buckle when the axis swayed in the wind, hence before the living contents are absorbed the walls are strengthened by lignification. A long specially strengthened

tube for conduction of water as it occurs in the plant is known as a vessel or vas. When the thickening is deposited in rings at regular intervals along the vas an *annular vessel* results. If the thickening follows a helical or spiral line up the internal surface of the tube, the structure is a *spiral vessel*, and if uniform over the whole surface except for pits, it is known as a *pitted vessel.* Such vessels, or vasa, are typical of the water-conducting tissue called the xylem.

Tracheids

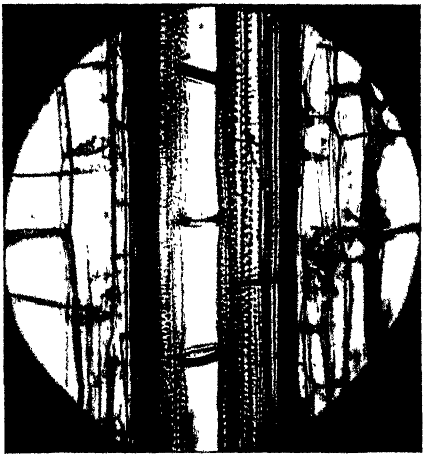
In some plants the xylem elements are not true vessels but elements of a less well-developed type. In the formation of these, the vertical line of cells does not lose the cross walls, but each cell elongates to resemble, in shape, a not too-well-developed fibre. When seen in transverse section the cells appear square, while in a longitudinal view they are lozenge-shaped with diamond-shaped ends. The walls are usually thickened and have many pits. True vessels are sometimes named *tracheæ*, hence these structures which approximate them are tracheæ-like or *tracheids.*

Elements for Food Conduction : Sieve Tubes

Somewhat similar lines of cells go to form the tubes used for the conduction of food from one part of the plant to another. The cross walls here are not completely dissolved out, but are pierced by large-diameter holes to form a sieve-like plate across the tube. This provides the sieve tube, the characteristic element of the phloem or food-conducting tissue. Associated with each length of tube—that is, from one plate to the next—is a companion cell. This results from the method whereby the units form. As a preliminary to the formation of the tube each cell of the line is divided into two by a longitudinal wall. Unlike a normal cell division, the nucleus does not divide but passes entire into one of the products. This cell which receives the nucleus is the companion-cell, while the other which receives no nucleus but only protoplasm goes to participate in the formation of the sieve tube.

These are the two main conducting tissues of the plant. First, the xylem for conducting the water and dissolved salts derived from the soil; second, the phloem for conducting true food. The first is recognized by the presence of vessels; the second by the presence of sieve tubes with companion cells.

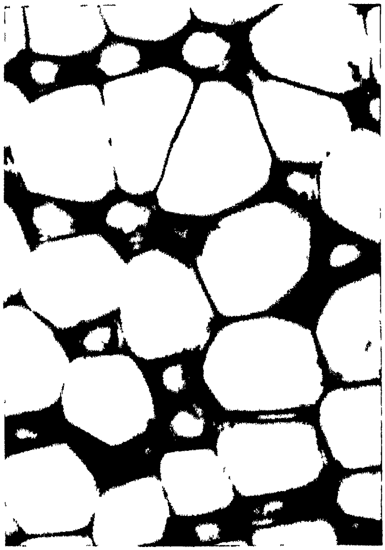
PLATE 7 XYLEM VESSELS



An annular vessel is seen in the centre of the photograph

Spiral (Sp.) and pitted (Pit.) vessels. An intermediate type with close or tight spiral (T. Sp.) thickening lies between

PLATE 8 PHLOEM ELEMENTS



Phloem cut transversely. (*Left*) Two sieve plates are seen; (*Right*) A number of sieve tubes (large and empty) each with a companion cell (small and full)

Phloem cut longitudinally shows two sieve plates

Tissue Systems

Usually the elements of the xylem and phloem are accompanied by packing cells of parenchyma or strengthening cells of sclerenchyma. Such a unit, composed of a mixture of different elements but engaged in one particular function, is called a tissue system. The xylem as a whole (vessels with associated parenchyma, and sclerenchyma) is a tissue system. Reference may be made to xylem-parenchyma or xylem-fibres when these elements occur associated with lignified vessels or tracheids. So, too, the unit engaged in food conduction and composed of sieve tubes, companion cells, phloem parenchyma, and phloem fibres, is the phloem tissue system. The phloem is sometimes called the bast; hence the term bast-fibres is often used.

Special Tissue Elements

The only remaining types of tissue element requiring mention are not essential constituents of a plant but often occur.

Sclerides

Individual cells with thick, hard walls sometimes appear isolated in otherwise soft tissue. These isolated elements do not constitute a sclerenchymatous tissue, but each is known as a *scleride* or *stone cell.* The "gritty" consistency often noticed in the soft flesh of a pear is caused in this way.

Lactiferous Tubes

The so-called lactiferous tubes or latex vessels in appearance are long tubes somewhat similar to vessels, but formed in a rather different way. They carry, not watery solutions, but a milky juice or latex. This is seen when the tissues of a dandelion are cut across and a white latex "bleeds" out. The latex of a number of different plants when extracted and processed makes the rubber of commerce.

Glandular

Another tissue is the glandular, which secretes various substances. The glandular and lactiferous may be associated to form long tubes lined along their length by glandular cells.

THE MORE IMPORTANT TISSUE ELEMENTS

Summary of how they are formed and description of their essential character

Tissue elements: each unit formed from an individual cell

give rise to

MERISTEMATIC CELLS PRODUCED BY MITOTIC DIVISION

give rise to

Tissue elements: each functional unit formed from more than one cell

Any Section

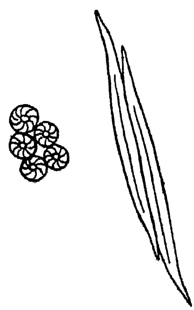
PARENCHYMA. Cells spherical (isodiametric). Living contents, vacuoles, and intercellular spaces present.

PARENCHYMA with walls thickened uniformly except for pits. Living contents present.

T.S. L.S.

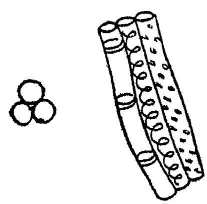
COLLENCHYMA. Cells elongated, and wall thickened locally towards intercellular spaces; living contents present.

PROSENCHYMA. Cells considerably elongated. Walls thickened with cellulose; may be pitted. Living contents disappear.

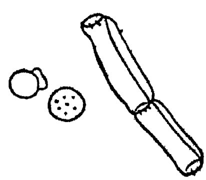


SCLERENCHYMA. Practically identical in appearance with prosenchyma. Walls not pure cellulose.

XYLEM VESSELS formed from a row of cells parallel with long axis of organ. Units variously thickened.



PHLOEM; sieve tubes and companion cells.



Tissues must be identified by their Elements

It is of importance that in interpreting a microscopic preparation, tissues and tissue systems should be recognized and delimited by the presence of the typical elements. It so happens that the tissues and tissue systems are usually arranged in the various organs in a perfectly definite manner and in the same spatial relationship one to the other. Students are often tempted to "recognize" tissues by their position in sections. Some plants, however, do not conform to the usual or standard pattern, and hence errors occur in describing these anomalous forms.

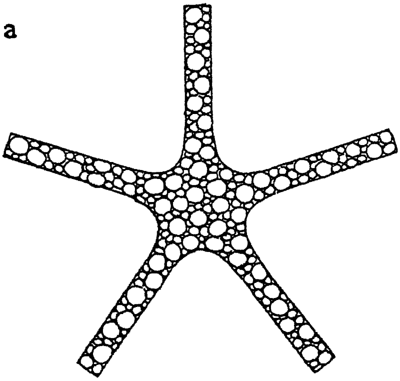
Arrangement of Tissue Systems in a Dicotyledon

As has been said, these various tissue elements when grouped to serve a definite function constitute a tissue system. The various tissue systems occur as discrete parts or regions in the various organs, all being disposed in definite ways. It is to the typical arrangement of tissue systems in the dicotyledon we now turn. For this purpose, sections in the three possible planes—T.S., L.R.S., and L.T.S.—must be examined. It is to be remembered that the axis is cylindrical, therefore we may refer to its centre, that is, the line running up the middle and also to its radii extending in a straight line from the centre to the outer layer.

The Transverse Section

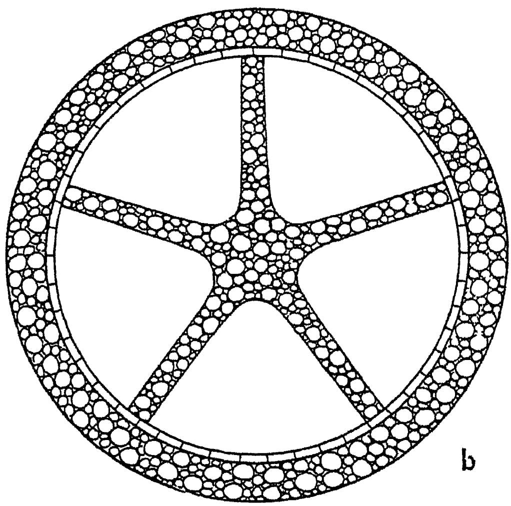
In the centre of the stem is seen a tissue of purely parenchymatous elements. This is the pith or *medulla*, which occupies a central position the whole length of the axis. Running out transversely from this are narrow rays of parenchyma, the medullary rays. The medullary rays pass outwards till they meet a ring or belt of parenchyma called the cortex. Occupying the space bounded on either side by medullary rays, internally by the medulla and externally by the cortex, is one vascular bundle. In transverse section, the bundles are seen to be equal in number to the medullary rays and to be on radii alternate with them. The bundles form a ring of " islands " round the central medulla, each being separated from the other by a medullary ray and all equidistant from the centre. Immediately outside the ring is an ill-defined layer, the *pericycle*, then comes the continuous ring of the cortex. Outside the cortex is the skin or epidermis.

a



(*a*) The central medulla and medullary rays.

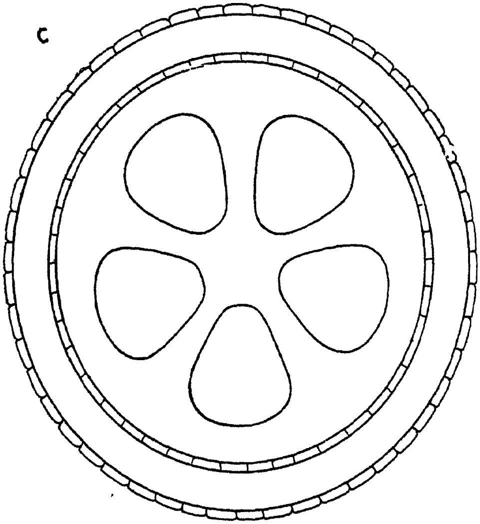
(*b*) The medulla, rays and cortex.
The specialized innermost layer of the cortex is the endodermis



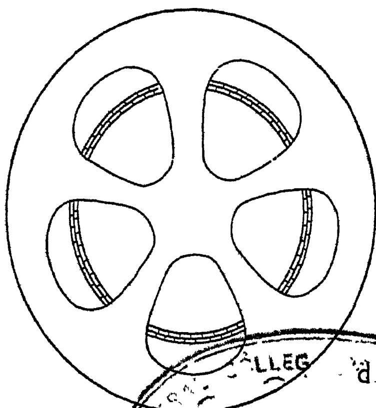
b

Fig. 19

c



(*c*) The vascular bundles in a ring.
The region between them and the endodermis is the pericycle



(*d*) The stele, all the tissues internal to the endodermis. Each bundle shows xylem, cambium and phloem

FIG. 19

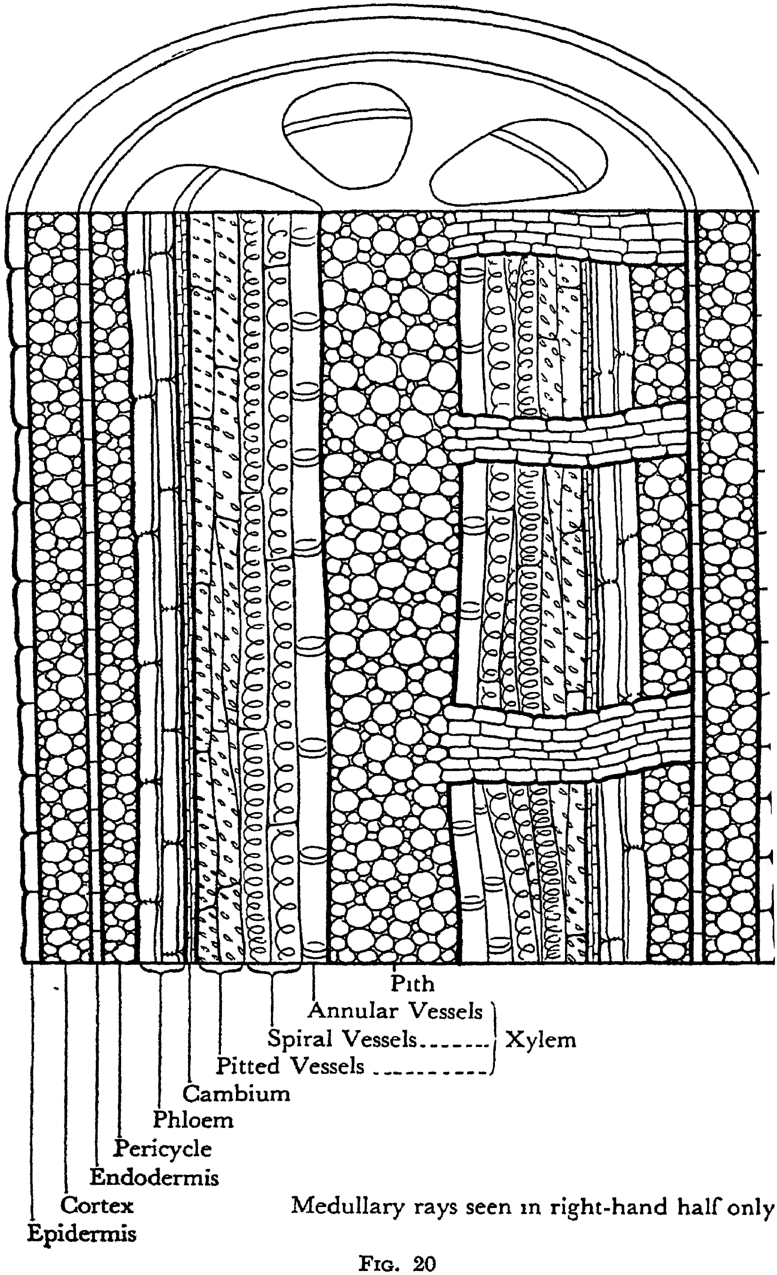


FIG. 20

Dicotyledon stem : the L.R.S. in relation to the T.S.

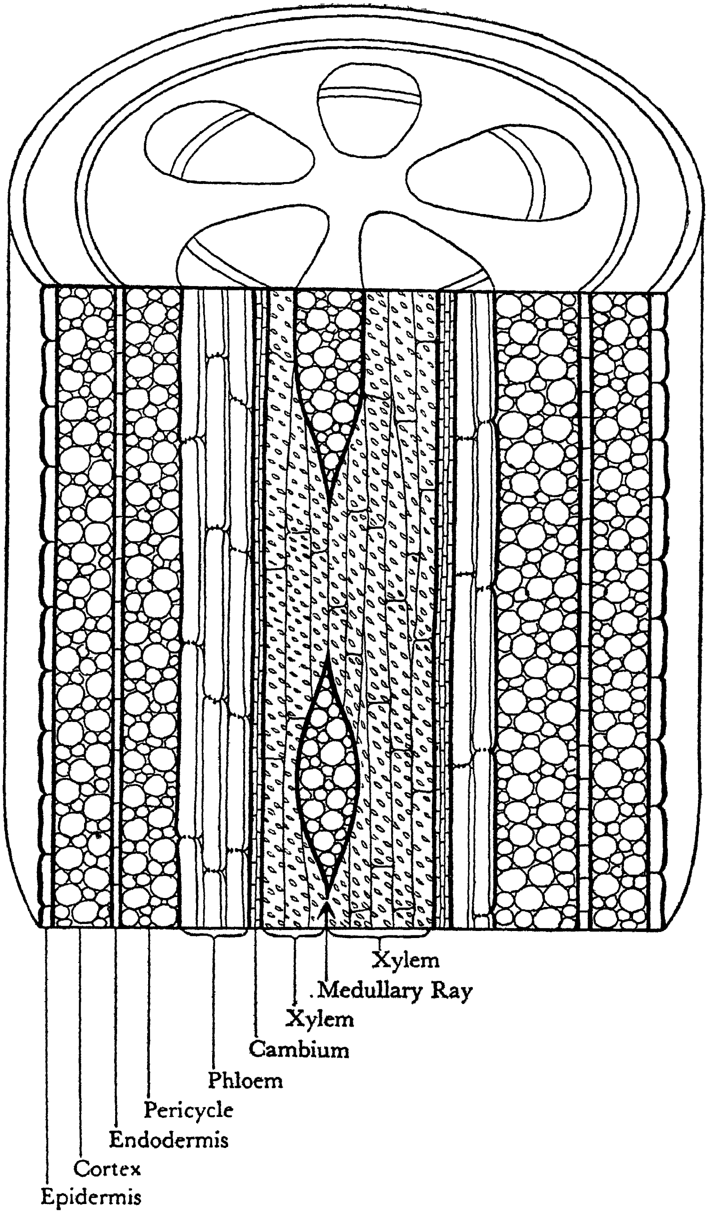


FIG. 21
Dicotyledon stem : the L.T.S. in relation to the T.S.

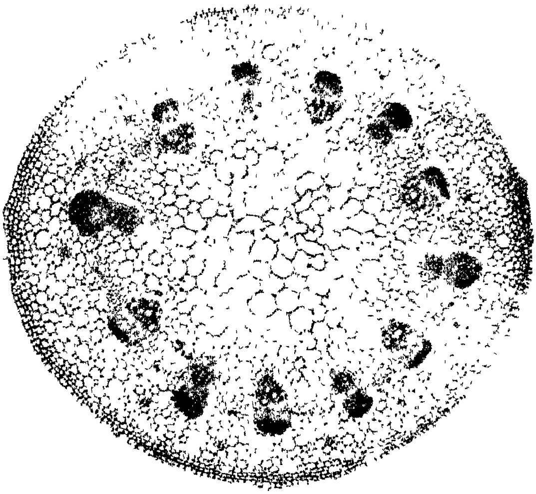
COLOUR PLATE I

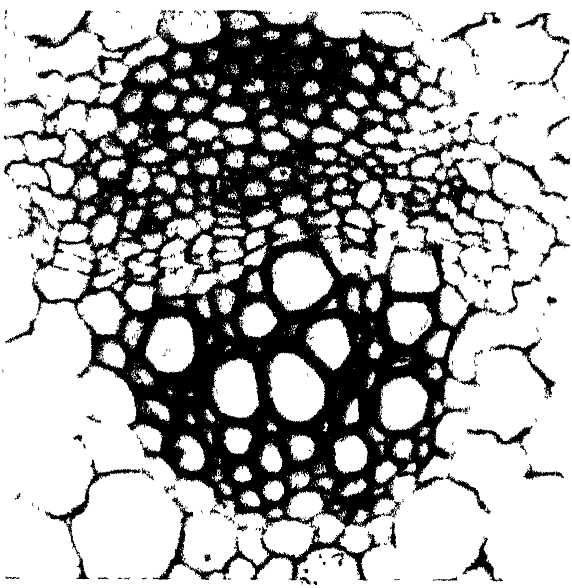
ANATOMY OF A DICOTYLEDON: THE STEM IN TRANSVERSE SECTION

Upper : The whole section is under intermediate magnification, the wide pith lying centrally is composed of parenchyma. The vascular bundles—twelve in number here—are arranged in a ring. The pericycle is ill-defined and lies outside the ring of bundles. The cortex, formed of parenchyma, extends from the pericycle outwards to the epidermis, which is the outermost layer and is one cell deep. Extending from the pith to the cortex are the medullary rays. The darker stained (blue) band of cells running round the section through the bundles and across the rays is the cambium

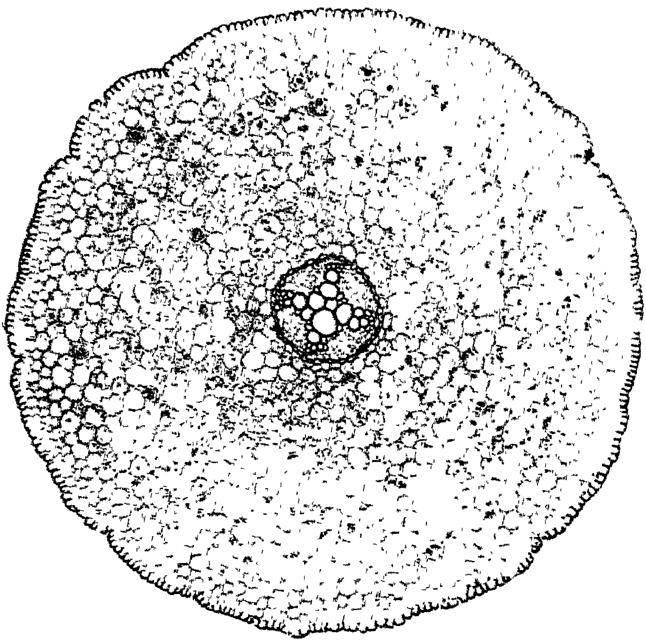
Lower : One bundle is magnified under higher power, lignified tissue stained red. The xylem elements (vessels), somewhat angular in outline, are towards the inner (lower) aspect. Above them, in the plate, lies a thin band of regular thin-walled cells—the cambium. Outside the cambium is the phloem, stained blue. In the phloem the large diameter elements are sieve tubes ; the smaller elements which accompany them are companion cells. External to the phloem the large mass of deeply stained (red) tissue is sclerenchyma. This bundle is collateral, that is to say, the xylem and phloem lie on the same radius. Collateral bundles in a ring, wide pith and narrow cortex, are typical of dicotyledon stem structure

COLOUR PLATE I





COLOUR PLATE II
ANATOMY OF A DICOTYLEDON: THE ROOT IN TRANSVERSE SECTION



The whole section is under intermediate magnification. The outermost layer of cells is the piliferous layer, and within this lies a wide parenchymatous cortex, the cells of which are filled with dark-stained starch grains. The endodermis, one cell deep, lies between the cortex and stele and is well marked. Within the stele the red-stained area includes the phloem. The phloem groups are on alternate radii with the dark-stained arms of the xylem. (The cambium is not well marked in this section.) Radial bundles, narrow stele, and wide cortex are typical of a root structure

The innermost ring of cells of the cortex, that is the one in contact with the pericycle, is specially identified, for often (more apparently in the root) the radial wall of each cell is thickened with suberin. This little strip is called the *casparian strip* and the ring of cells is called the *endodermis*. All the tissues internal to the endodermis constitute the *stele*. A summary of these various regions may be made by following in the transverse section one of the radii on which a bundle occurs. At the centre is medulla, then bundle, then the region of the pericycle, then the endodermis, then the mass of the cortex, and finally, on the outside, the epidermis. This general layout of tissue and tissue systems is typical of the dicotyledon axis, though small differences occur between root and shoot.

The Arrangement of Tissues in the Vascular Bundle of a Dicotyledon

Little need be said about the medulla and its rays. The bundles attract most attention. Rather more than half the bundle is xylem, and this tissue lies on the inner aspect towards the central medulla. The phloem lies on the outer aspect of the bundle next the pericycle. Between the xylem and phloem a few cells will be seen which are thin-walled and full of living contents. This small region of typical meristematic tissue which has persisted with its cells unmodified since the stem was made by the primary meristem is called the *cambium*. Because it is a direct persistence of the original meristem it is called a primary cambium. The presence of a cambium is of considerable significance and is typical of a dicotyledon, its function is to add new cells as required to thicken the axis. This means the bundle is open for further development and may be described as an *open bundle*.

The bundle in the stem is therefore composed of xylem internally, cambium in the middle, and phloem externally. All three tissues lie on the same radii, and the bundle is called a *collateral bundle*.

The Longitudinal Section

What may be seen in longitudinal section depends on whether the cut is radial or tangential. When the radial section (L.R.S.) passes through a medullary ray, this structure is seen to be continuous from centre to cortex but only a few cells deep. Unlike the other tissues of the axis, the rays are not continuous from top to bottom of the axis. Rather they may be pictured as arms

running out laterally from the central core of medulla like the arms of a many-armed fingerpost.

In the tangential section (L.T.S.) the rays are seen cut across as the spokes of a wheel would be by a tangential cut.

The pith or medulla then is a continuous central core, supplied with arms or rays which run out to connect with the cortex. The function of this structure is to provide a path between the exterior and the inner tissues for transverse conduction ; gases in the intercellular spaces, water and dissolved substances from cell to cell. All the other tissues run continuously from apex to base and show their characteristic elements as already described.

The Tissues of the Dicotyledon Root

When this disposition of tissues in the dicotyledon stem is compared with that in the root of the same plant, only two differences are remarkable. These are clearly seen in T.S. As in the stem the xylem is nearer the centre than the phloem, and the cambium is between them, but the xylem and phloem groups instead of being on the same radius are on alternate radii. The bundles of the root therefore are not collateral but radial.

The second difference is that the medulla in the root is considerably reduced so that the bundles are brought much nearer the centre. Put otherwise, in the root the stele is narrow and the cortex is broad, while the converse is true of the stem.

This difference in disposition of the tissues is connected with questions of mechanical efficiency. The xylem elements are strong, and it is to be remembered that most of the fibrous elements run alongside the conducting elements up and down the axis. The fibro-vascular tissues can be pictured as ropes stretching from a point just below the tip of the stem down nearly to the tip of a root. The significance of their internal disposition in the root and more nearly external disposition in the stem can then be seen. As the stem sways in the wind it bends at the soil level. The " ropes " in the stem have to be out to the exterior, working over the fulcrum of the pith, if they are to pull the swaying axis back to the vertical. In the root the " ropes " have to be as near central as possible so as to give a firm anchorage. The transition region where the bundles run in from near the skin to near the centre is at or about soil level. This region of transition in the axis is mainly in the hypocotyl.

All these tissues of the mature axis are derived by modification from cells formed by mitosis in the primary meristem at the shoot or root tip. The anatomy of these apical regions of the axis are best studied in a median longitudinal section, *i.e.* a longitudinal section in the plane of a diameter.

The Stem Apex

The extreme shoot-tip is a mass of very delicate undifferentiated tissue. The first sign of differentiation is seen a little way behind the tip. Here the outermost layer of cells takes on the character of an epidermis. The cells remain very close together with no intercellular spaces, and are regular in shape. This layer is called the skin producer or *dermatogen.*

Within this is a layer some few cells deep called the *periblem.* It will form the cortex. Inside the periblem is a central core of cells, the *plerome.* From the plerome develop all the components of the stele. These three layers, dermatogen, periblem, and plerome, are the primary *histogens.*

If a slightly older portion of the young stem is examined, the dermatogen will be seen to form little humps by cell division. As older and older levels are examined the humps get bigger and bigger, until they are seen each to be a leaf with a bud in the axil. Leaves and buds are formed from superficial tissues. They are said to be *exogenous* in origin. As the leaves get older they grow by cell division at their bases and curl upwards to overlap the young tissues above them. This forms a bud. The meristematic tip of a shoot is protected by overlapping leaves.

The Root-Tip

In the root the meristem is as in the stem, and differentiates into the three layers or primary histogens as described, though of course no leaves or buds are produced by the dermatogen. In addition to providing cells behind the tip for elongation of the axis, however, the meristem at the very apex produces a mass of cells in front of itself. This forms a protective cap called the root-cap. As the root pushes its way through the gritty soil, the cells of the outside of the cap are rubbed off, but the group of cells is constantly added to on its inner side by the continuing activity of the meristem.

Origin of a Branch Root

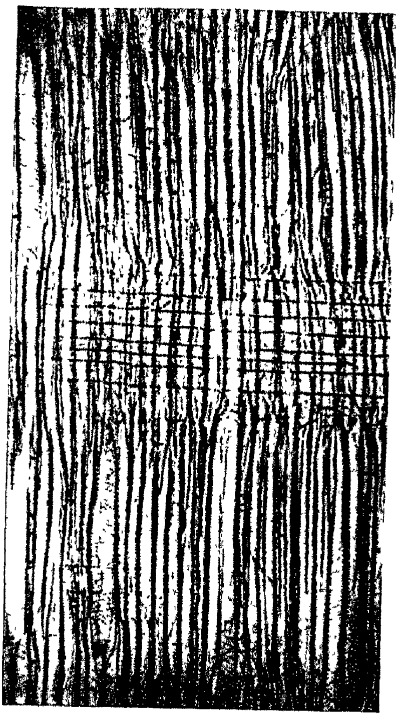
When an older portion of the young root is examined, the origin of a branch will be seen. A small group of cells of the pericycle opposite an arm of the xylem commences to divide actively. By this means a lateral growing point is formed. This, by its continued growth, pushes its way outwards from the deep tissues of its parent through the endodermis, cortex, and skin to the exterior. Conducting elements differentiate in the lateral and connect with those of the parent root. Branches of a root are of deep or *endogenous* origin, not as in the shoot, where they are superficial or exogenous.

The Developmental Zones of the Root

From what has been said, it emerges that successive transverse sections taken from the tip backwards up the root will cut through zones at different degrees of development. These zones may be roughly delimited by inspecting a young intact rootlet under a hand-lens. The root used must be intact. To get this it must be grown and produced in moist air. If taken from soil, the contact between the earthy particles and the root is so intimate that it is impossible to separate them without damage. Examination of a suitable specimen will show the root-cap in outline. The axis for some way behind the actual tip will be smooth and glistening. This is the zone where the primary histogens are taking shape. Behind this zone, the surface becomes more and more covered with hair. The hairs nearest to the tip are youngest and shortest. The hairs farther up the root are older and longer. After the region bearing the longest hairs is passed the outer surface of the root becomes smooth and brown. Inside the hair-bearing zone, differentiation of the tissues is proceeding, and a section taken in the region of the longest hairs will show fully developed vascular bundles. Practically the whole of the water absorbed by the root is taken in through the hair-bearing zone. Above the hair zone the skin of the root is of a cork-like nature, almost impervious to water ; below the hair zone the root is too young for maximum function. As the root lengthens the zonation goes forward. As the hairs age they die and the root surface modifies. New hairs develop on the younger zone.

PLATE 9 LATEX TUBES AND TRACHEIDS

Latex tubes in Dandelion



Tracheids in longitudinal radial section of Lime Wood. The rectangular cells running across the section are those of a medullary ray

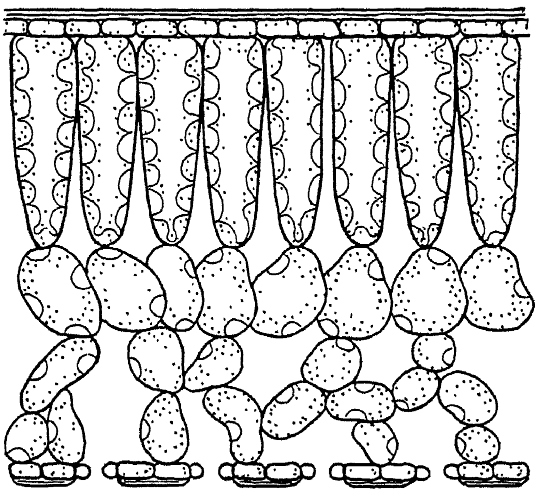
PLATE 10 THE ROOT

Seedling : Note the three zones of the root

Root hairs of Lucerne (highly magnified)

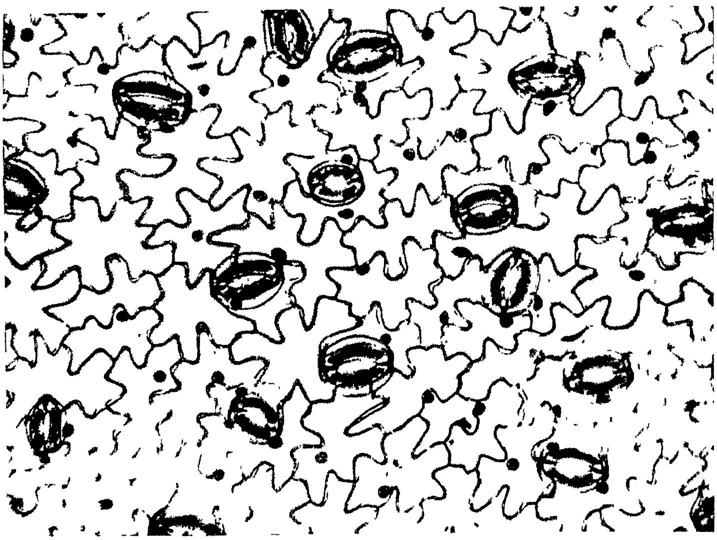
PLATE 11 LEAF ANATOMY

Vertical Section: From above downwards—almost transparent cuticle, upper epidermis, palisade parenchyma, spongy parenchyma, lower epidermis with two stomata cut across



A diagrammatic representation of the same

PLATE 12 THE LEAF EPIDERMIS
(Dicotyledon type)



Surface preparation. The only intercellular spaces are the stoma pores. Only the guard cells contain chlorophyll

A portion of the above more highly magnified. General cells, round with irregular outline, no green colour, large nucleus; guard cells much green colour and large nucleus

Root Hairs

When seen under higher magnification each root hair is seen to be a tube-shaped out-thrust of the wall of an epidermal cell. Unlike other unicellular hairs they are very highly hydrated, and the nucleus of the cell is in the shaft of the hair. The important point is that by bulging outwards in this way the cells of the skin of the root increase very much the total surface the root exposes to the soil and its water. One might liken this part of the surface of a root to the coastline of a country. If the coast has no peninsulas and arms of land running out into the sea, the total coastline is quite short. If, however, there are many peninsulas and out-thrusts of the land the coast is much indented, and the actual amount of contact, land to sea, is very large. The root hairs are out-thrusts from the root surface into the interspaces of the soil. It has been calculated that the ratio of surface of a root with hairs to that of a root without hairs is as high as 18 : 1. The value of root hairs to the plant is apparent when it is remembered that the amount of material absorbed across a surface is proportional to its area, other factors being constant.

The density of hair, and the length of the individual hairs, varies with circumstances. Where there is plenty of water they may be few and short or absent. As progressively drier soils are occupied, the hairs progressively increase. When the soil is so dry as to render the production of such an increased surface dangerous as an agent of water-loss rather than gain, the number and size of the hairs falls. It is interesting to notice that in a soil with the proper amount of water (soil air fully charged with water-vapour but not displaced by liquid water) the contact of the root hairs with the soil particles is very close. The mucilaginous walls " flow " or bulge round the soil particles and partially surround them. The root hair not only increases surface but gives very intimate contact with the soil.

Water and manurial-salt intake is restricted, almost completely, to this area where the root hairs can and usually do occur. The very youngest portion of each root is engaged in growth and development and not fully organized for effective intake. Above the hair area, the epidermal layer is either so modified or replaced by another structure that entry is prevented. The skin or true epidermis of a root, because it bears hairs of such great significance, is usually called the *piliferous layer*.

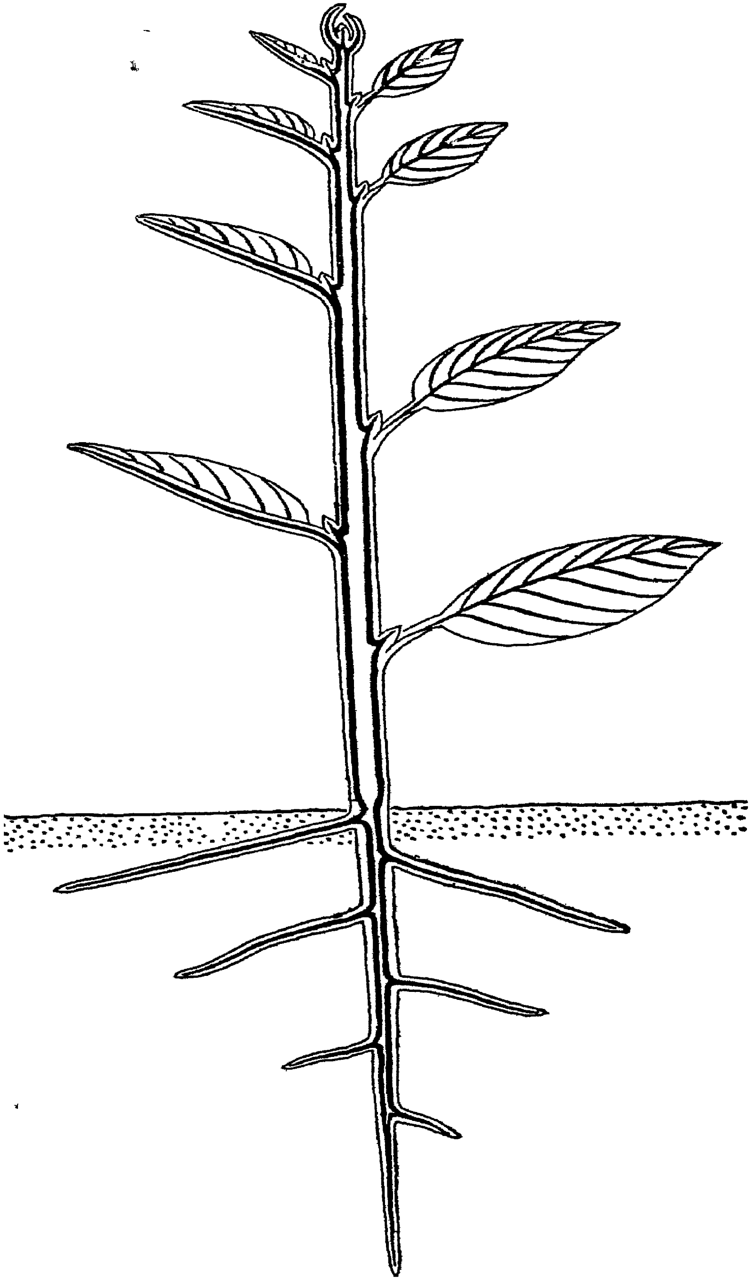


FIG. 22
The conducting tracts are continuous

The picture, then, we have of the dicotyledon root is of a central axis with branches like itself, providing a powerful anchorage in the soil, acting as a conducting tract between the distal absorbing region and the shoot. As the root-tip grows out, exploring a greater and greater volume of soil, the absorbing region develops behind, exploiting always fresh " feeding ground." As it occupies new areas downwards and outwards, internal modification carries the conducting tracts always behind. The conducting tracts run continuously up from the root and into the stem, passing out to branches and up through the leaves, so that the conducting system of the plant is continuous throughout from the finest branch root to the tip of the farthest leaf, just as we might say the railway lines of a great railway system are continuous. One might start at a very lonely country siding and follow the lines back to the big main trunk routes, through the marshalling yards, and out to the last little sidings in another area ; there is no break in the lines along which transport is carried.

The Leaf

The main points regarding the morphology and anatomy of root and stem having been covered, the leaf requires brief treatment. As has been shown, the leaf is a development for the trapping of light energy. In addition, it is the organ primarily involved in the exchange of gases from the tissues to the outer air, and from the air into the tissues. The leaf accordingly is normally a flat, expanded structure, and if the intake and output of gases along with absorption of light energy were its only problems, then a large flat structure one cell deep would be the ideal. However, the leaf must occupy a position up in the air resisting gravity, wind damage, etc. It must be strong and tough. Further, it must provide accommodation for the conducting tracts, bringing up water or taking away food, and hence has to have some thickness. The leaf, then, is some cells thick and in area must be adjusted, within certain mechanical limits, to the over-all size of the plant. The demand that the greatest possible area of shoot system be exposed to light is met by the flat, expanded shape of the leaves. These should not overshadow one another, and a great variety of modifications of shape and arrangement on the stem have developed for this purpose, but the actual make-up of the tissues in most leaf blades shows few variations, and

they conform very closely to a standard pattern, and this is our immediate study.

Leaf Venation : Dicotyledon Type

When the blade of a dicotyledon leaf is held between a strong light source and the eye it will reveal its " skeleton," just as a human hand might when placed in an X-ray apparatus. It will be seen that a main-vein, or main-rib, as it is called, enters from the stem and passes up into the lamina. Here it branches. The arrangement within the blade varies in different kinds of plant, but commonly there is one main-rib running centrally from the base to the apex of the leaf, and from it come branches which themselves branch and rebranch. The finer members curve and twist and run together. The ribs and veins, with their finer branches, the venules, form a network called, collectively, the venation. The venation as a whole serves three functions : mechanical support, conduction in of water and dissolved salts as well as conduction out of food. The duplication of terms, " veins " and " ribs," arises from this. In the sense of a skeletal function, the thicker units are called ribs, in the sense of conduction, veins. The simplest terminology is mid-vein or main-vein, branch vein, and venule. The whole system forms a network or *reticulum*. The venation of a dicotyledon leaf is, with few exceptions, reticulate.

Anatomy of a Dicotyledon Leaf

When a vertical section is cut transversely to the main vein, the tissues of the leaf may be examined. In such a section the first point of reference is the main-vein itself, for it will be cut transversely ; all other veins may be cut in all sorts of aspects, from transverse through oblique to longitudinal, depending on the course followed by each at the plane of the section. The main-vein consists of xylem and phloem. As the xylem in the stem is internal to the phloem, and as the vascular bundle of the stem seems to bend over and outwards as it runs into the leaf, the xylem appears above the phloem in the veins. Thus it is always possible to tell the upper from the lower surface of a leaf in section by examining a vein. Cambium rarely occurs in the vascular bundle of a leaf except in such kinds of plants as do not cast their leaves every autumn—evergreen plants. Otherwise the

COLOUR PLATE III
ANATOMY OF THE APEX OF STEM AND APEX OF ROOT

A Stem Tip

The meristematic cells are at the uppermost point. These delicate cells are protected by overlapping leaves which arise at lower levels. Note that the lateral members of a stem arise from superficial tissues

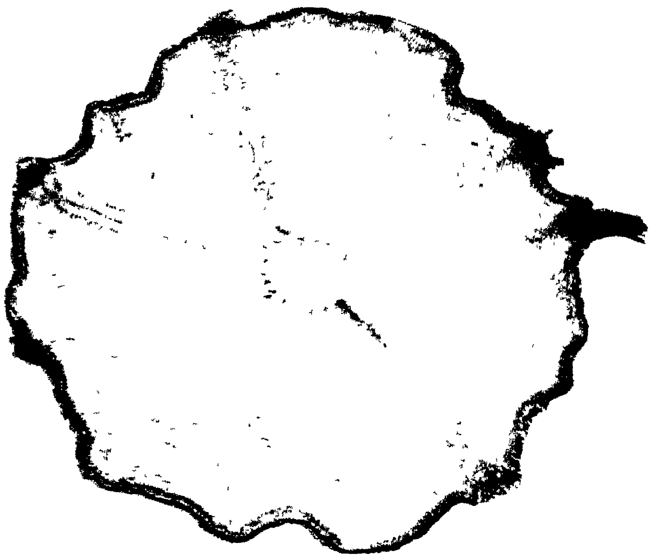
A Root Tip

The meristematic cells are at the base of the most deeply stained part in this plate. By their activity they produce tissue externally which forms a protective cap, and also produce tissues internally which form the permanent elements of the roots

COLOUR PLATE IV
ROOT ANATOMY: ORIGIN OF A BRANCH ROOT

Above: T.S. of a main root at a level where a branch is just forming; intermediate magnification. Cells of the outer layers of the stele (pericycle) become active at a point just opposite a xylem group. A growing point is formed and the young root presses out towards the exterior

Below: A main root cut transversely (the branches are cut longitudinally)



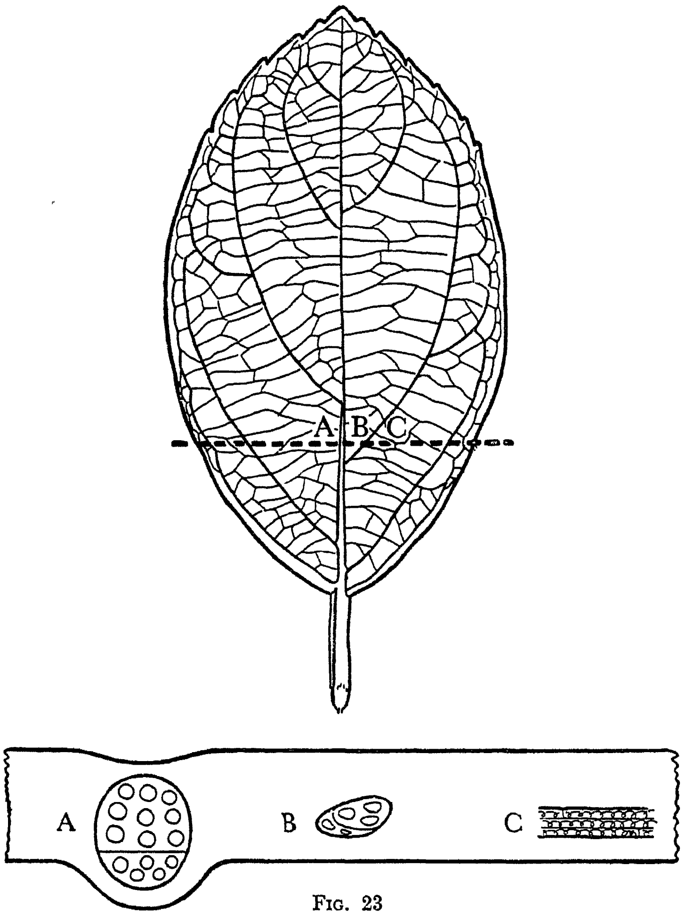


FIG. 23

T.S. of a dicotyledon leaf (reticulate venation) showing veins cut in different ways—transversely, longitudinally, and obliquely

vein of a leaf is constructed of the same elements, and in the same way, as a vascular bundle of the stem, though it differs slightly in being surrounded by a layer of parenchyma called the bundle-sheath. Between the two epidermi, like the filling of a sandwich, lie the mesophyll tissues.

The Epidermis of the Dicotyledon Leaf

The whole outer surface of the leaf, like that of the stem, is bounded by a layer of cells one cell deep. This constitutes the upper and lower epidermis. The epidermal cells seen in section are brick-

like with only occasional intercellular spaces. When such a space does appear it is bounded by two special cells. The general cells of the epidermis are covered on their external walls by a hard, transparent varnish; this is the cuticle. In different leaves the cuticle varies in thickness. The general cells of the epidermis are supplied with living contents but are devoid of green colour.

The Mesophyll of the Dicotyledon Leaf

(1) *The Palisade.*—Immediately below the upper epidermis lies a layer of cells, each one of which is shaped like a short column, with the long axis of the column perpendicular to the leaf surface. In transverse section the cells appear to be packed tightly with no spaces between them, and so resemble a palisade. As they have thin walls and living contents, they are parenchyma; the so-called palisade parenchyma. The likeness to a palisade is misleading, for if one looks downwards through the upper epidermis at this tissue it is seen that there are many intercellular spaces. These spaces run parallel with cells, and so do not appear clearly in vertical sections.

(2) *The Spongy Mesophyll.*—Below the palisade parenchyma lies a parenchymatous tissue with many very large intercellular spaces ramifying in all directions. This layer somewhat resembles a sponge; the cells being the fabric and the intercellular spaces the holes of the sponge. This tissue is called the spongy parenchyma.

The Lower Epidermis

Below the spongy parenchyma lies the lower epidermis, very similar to the upper epidermis, but usually more richly supplied with the peculiar intercellular spaces already alluded to. It is to be noted that these intercellular spaces are like little tunnels or corridors passing through the epidermis, and connecting the outer air with the air in the intercellular spaces inside the plant. They are the channels through which gas passes between the air of the intercellular spaces (internal atmosphere) and the atmosphere surrounding the plant (external atmosphere). Thus, because every intercellular space inside the plant connects with at least one other, the whole of them form a continuous system. The intercellular spaces are like a continuous network with its ends running out through the epidermis. The cells form another network, the two being interwoven together. The important fact

is that any particle such as a gas molecule capable of moving in air can pass from the outside into the plant, and so to any part of it. So too can a similar particle pass outwards.

The Leaf as a Light Trap

The upper epidermis with its cuticle, being almost transparent, allows light to pass through to the long columnar cells of the palisade. Each cell of this tissue is richly provided with small dense pieces of protoplasm something like nuclei and called *plastids*. These are coloured green by the presence of the special pigment of green plants called *chlorophyll*. A plastid bearing chlorophyll is called a *chloroplast*. It is the chlorophyll which absorbs light. The chloroplasts congregate on the long walls of the palisade cells, so that the greatest number have light-rays impinging on them. If they massed on the ends of the cylinder, only a few could be accommodated there, and these would be in full light and the remainder would be in their shadow.

The Leaf as a Food-making Factory

The palisade, accordingly, is the place where most of the light energy is trapped and fixed into food; it is the main locus of food-making, to be discussed in Section Two. Water is drawn into these cells from the xylem lying in the veins at their bases. The carbon dioxide gas they use in conjunction with the water and light for food-making, moves easily in through the intercellular spaces of the lower epidermis, along the pathways of the intercellular spaces of the spongy parenchyma, and up the spaces between the columns of the palisade parenchyma. There the gas dissolves in the water of the cell wall and passes through to the chloroplasts. The chloroplasts on the long walls are therefore ideally placed, not only for light supply, but also for gas supply.

The palisade is predominantly the region of food synthesis. The cells of the spongy parenchyma contain a few chloroplasts, but this tissue is designed more to facilitate gas movement and distribution rather than the carrying out of food synthesis.

The Cells of the Leaf Epidermis: Dicotyledon Type

The epidermis of the shoot requires special study. The details are best seen in the lower epidermis of the leaf. To see these a portion of this skin should be stripped off and laid flat on a

microscope slide. This is called a surface preparation. At the same time a vertical section of the leaf should be prepared. In the surface preparation the ordinary cells of the epidermis appear as somewhat roundish but very irregular in outline, rather like the slabs of a very crazy pavement. The irregularities of one cell, however, fit very closely into the irregularities of its neighbours. *There are no intercellular spaces between them.* Each cell is supplied with protoplasm and nucleus, but is completely *devoid of chloroplasts and quite colourless.*

When seen in vertical section the cells of the epidermis appear very regular in size and shape, brick-like in fact. Only the wall to the outside is thickened by its covering of transparent cuticle. This general surface of the epidermis, then, allows light to pass through practically unimpeded to the palisade lying below, but the passage of a gas or water vapour is restricted to a greater extent by thick cuticle and to some extent by a thin one.

The Stoma : Dicotyledon Type

At intervals special cells appear amongst the ordinary elements of the epidermis. These occur in pairs, and each pair constitutes a unit called a *stoma.* Between the cells of the stoma is a small intercellular space, channel, or pore—the *stoma pore.* This pore connects the outer air surrounding the plant with the air lying in the intercellular spaces of its tissues. Because the two special cells appear to guard this entrance to, or exit from, the tissues they are called the *guard-cells.*

A stoma, then, consists of an intercellular space or pore and two guard-cells. As seen in surface preparation, each guard-cell resembles a crescent moon with very blunt ends. The two cells lie with their long axes in the plane of the leaf surface and the concave sides facing each other. The two crescentic cells are attached together at the horns. The pore is formed between the concave aspect of the one and the concave aspect of the other as they lie facing each other.

In the vertical section the guard-cells are seen cut across and somewhat round or oval in outline. The pore in this section appears as a definite channel connecting the internal atmosphere with the external, for under it in the tissues is always a specially large intercellular space. Both guard-cells contain chloroplasts richly supplied with chlorophyll. Thus, *the only intercellular spaces in the whole epidermis are the stoma pores ; the only cells of the epidermis*

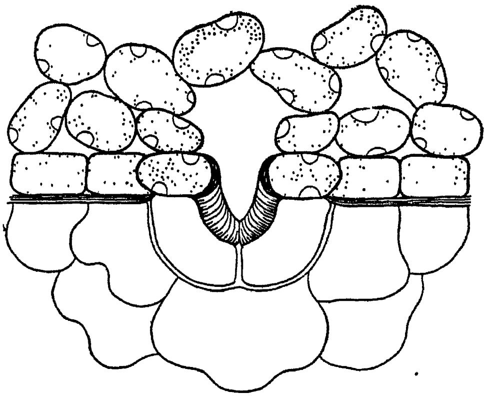


FIG. 24
The stoma in surface and V.S. views, seen obliquely from below

which contain chlorophyll are the guard-cells. The only path for gases or water vapour entering or leaving the leaf is the stoma pore.

How the Guard-Cell Functions

The guard-cells function as a control valve on gas movement in or out. Control is effected by the fact that the walls of the guard-cells are not uniform. The wall facing into the pore is much thickened and inelastic; the wall abutting on the ordinary epidermal cell is thin and extensible. Whenever the guard-cells absorb water they swell. In this swelling, the thin wall facing towards the epidermal cell stretches considerably; the thick wall lining the pore does not. This makes each cell more concave to the pore, which is thereby made bigger and rounder. Conversely, if the guard-cell shrinks, the elastic wall away from the pore contracts, while the wall towards the pore remains static. The guard-cells then tend to straighten out and the pore becomes much less round. When the shrinking process goes to its extreme, the cells are nearly straight and the lips of the pore approach. The pore in this state of affairs is closed. The mechanism causing the guard-cells to absorb water or lose it, and so swell or shrink, will be discussed later.

THE STEM: SECONDARY THICKENING

This completes the account of the body of the dicotyledon type in its younger state. As the plant grows, and the canopy of leaves increases, the stem and root have neither the conducting capacity

nor the mechanical strength to meet the increasing demands. The axis at least must add to its girth.

If the original tissues laid down by modification of cells derived directly from the apical meristem be called the primary tissues, primary xylem, primary phloem, and so on, then the tissues formed later must be called secondary, and the process secondary growth or secondary thickening.

The meristem first involved is that already seen in small groups lying between the primary xylem and primary phloem and called the bundle-cambium. If only these groups added tissue, the axis would increase irregularly and get out of shape. A complete ring of meristem is required. This circle is formed when the parenchyma cells in a line connecting one bundle-cambium with another across each medullary ray recover their embryonical or meristematic character. This inter-bundle secondary cambium, along with the primary bundle-cambium, now forms a complete ring when seen in transverse section. It is a cylinder, of course, in the whole axis.

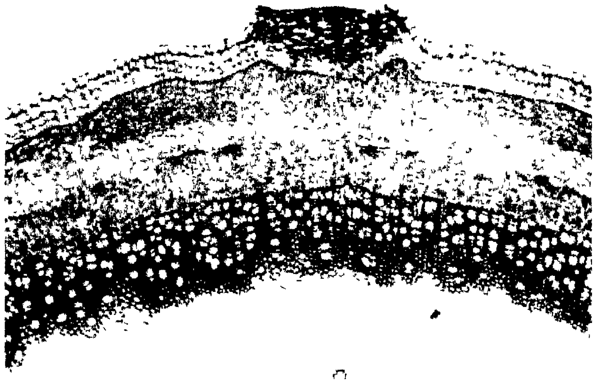
Cells of this whole cambium divide mitotically. The equatorial plate of practically every division lies on a line tangential to the ring. The cambium band therefore would increase in breadth, but the earlier formed cells of the ring promptly modify. The cells adjacent to the primary phloem form sieve-tubes and companion cells ; those abutting on the xylem form vessels, etc., while those crossing the medullary ray form parenchyma. The whole of the tissue systems increase together, and the stem remains a symmetrical cylinder.

Even this increase in conducting tissue fails to meet increasing demands for transport, and soon the products of the inter-bundle cambium change the nature of their modification. Instead of parenchyma they form xylem internally and phloem externally. Secondary bundles are thus formed. The proportion of medullary ray tissue in the axis progressively falls.

The further addition to the proportion of conducting tissue in the stems and roots so obtained may not yet be enough, especially in long-lived plants such as trees and shrubs. In these cases, almost the whole of the product of the inner face of the ring produces xylem or wood, while the outer face produces phloem. The medullary rays are now very narrow, the ratio of conducting tissue to parenchyma becomes very high, and secondary medullary rays may be formed when required. The stele thus increases in girth.

COLOUR PLATE V

ANATOMY OF A DICOTYLEDON: SECONDARY THICKENING AND CORK FORMATION



Transverse section of a stem under intermediate magnification

The external band of close-packed, square-shaped cells stained red is a layer of cork. These cells have been formed by the outermost layer of the densely stained (blue) cells immediately below. This layer is the cork cambium. Internal to the cork cambium is the product of its activity on the inner face, namely, secondary cortex. Below the secondary cortex is the original (primary) cortex. The xylem at this stage is almost a continuous ring, the medullary rays are very narrow. The original xylem groups are seen as out-thrusts into the pith. In the cork a breathing pore or lenticel is seen

In transverse section the amount of phloem seen is much less than the amount of xylem. This is usually due to the older non-functional phloem being crushed.

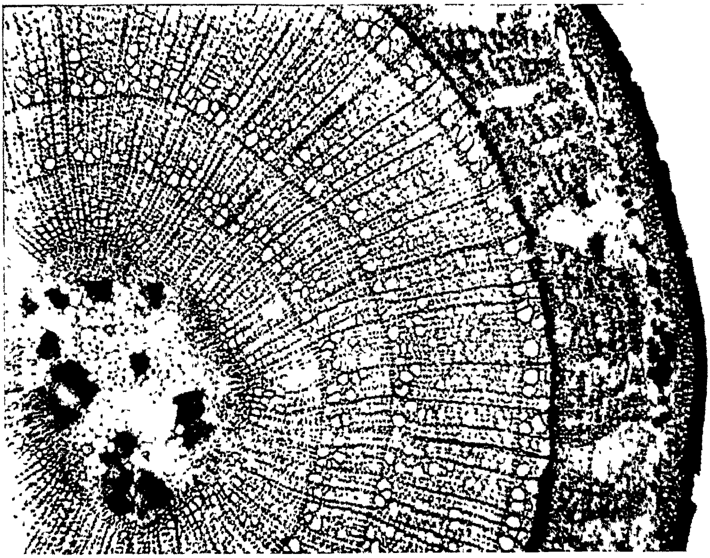
Annual Rings

The different tissues so produced are not uniform in character. The xylem vessels produced in late winter and spring are of large bore and packed around with a certain amount of parenchyma. In summer and early autumn the vessels are of fine bore and instead of paranchyma, more sclerenchyma is introduced. The product of activity in spring looks open ; the product of summer is dense. Thus every year in a perennial plant a complete ring of open tissue merging into a ring of dense tissue is produced. This is called an *annual ring*. When the stem of a perennial dicotyledon is cut across, the annual rings can be counted and hence the age of the plant decided.

Cork and Lenticel Formation

The increase of girth of the tissues of the stele may be very great, and as a result all the tissues external to it, cortex and epidermis would burst. They too must be either extended as well or have provision made for repair and replacement. This is done when a ring of cells, most often located in the cortex, resume the meristematic character to form a secondary cambium. This ring cuts off cells by tangential walls. The product of its inner face modifies to parenchyma and forms secondary cortex. The product to the outside forms a new kind of tissue. The cells over the greater part of the ring remain as formed, brick-shaped and with no intercellular spaces. The walls are changed by the deposition on them of a fatty product called *suberin*. The result is a very compact layer of tissue with suberized cell walls which is called *cork*. At points in the ring, or rather cylinder of this secondary cambium, the product consists not of brick-shaped cells but of spherical cells with the intercellular spaces carried to such a degree of development that the cells are really separate. Thus little channels are formed passing through the cork layers, each filled with dust-like loose cells. They provide little tunnels through which oxygen and other gases can pass to and from the outer air and the living cells of the tissues deep in the axis. A channel of this type is known as a *lenticel*. It provides a path

PLATE 13 STEM ANATOMY

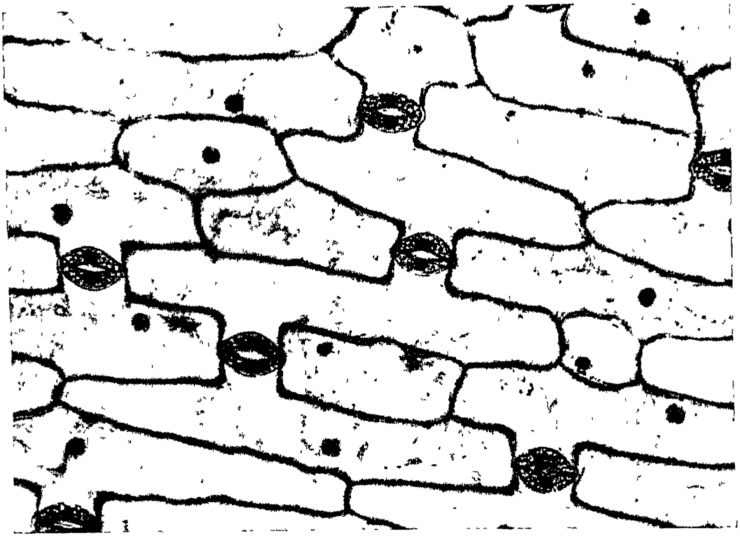


Secondary thickening in T.S. twig $3\frac{1}{4}$ years old. Three complete annual rings, fourth forming

Leaf abscission: L.S. stem cut in early autumn. Absciss layer at base of leaf

Wound healing: T.S. tree trunk, three branches lopped. The wound on right in process of healing

PLATE 14 THE LEAF EPIDERMIS
(Monocotyledon type)



Surface preparation

A portion of above more highly magnified. Note the shape of the epidermal cells, each with large nucleus and no chloroplasts. The guard cells have each a nucleus and many chloroplasts

for gas movement, and in this it resembles a stoma pore. A lenticel differs from a stoma in structure, and also in the fact that it is rigid and cannot open or close.

Of the two secondary cambiums, the one having cork as its main product is called the *cork-cambium ;* the other producing largely wood is the *wood-cambium.* Commercial cork used for stoppers, etc., is got from a kind of oak which develops a very active cork-cambium. Sometimes the product of the cork-cambium is called bark, but this hardly fits the facts. When bark is stripped off a plant, all tissues external to the wood-cambium come away, and therefore the term bark should be used to include all tissues external to the wood-cambium, *e.g.* secondary phloem, primary phloem, pericycle, primary cortex, secondary cortex, cork-cambium, cork, and the remains, if any, of the epidermis. The first cork-cambium is often replaced by a new one arising deeper within the stem.

Abscission and Wound Healing

The function of a cork-cambium is to provide a protective layer on the outer surface of the functioning tissues whenever they may become exposed either by accident or by natural rupture. The necessity for such protection is often anticipated, and provides another example of the beauty of the organization shown by living things. For example, when an obsolete organ is to be discarded, like a leaf destined to fall in autumn, a protective layer must be provided to cover the wound. Some time prior to the actual fall of the leaf, the event is anticipated and a peculiar layer forms at its base. A layer or plate of cells across the lowest level of the leaf base begins to break down and die. Just behind this layer, nearer to the stem, a plate-like layer of cork forms. This dual layer, or *absciss layer,* is completed by autumn and then the dying leaf is attached to the stem only by the epidermis and the still unbroken vascular strands. Soon these snap, and the leaf falls, leaving a scar shaped in outline like the transverse section of the base. The ends of the bundles which supplied the leaf appear as little dots on the surface of the scar. This can be seen very clearly in the horse-shoe-shaped leaf scars on a twig of horse-chestnut in winter condition. The " nails " of the shoe are the snapped ends of the vascular bundles.

In a dicotyledon, if a branch or twig is cut off as in pruning,

the cells of the wood-cambium are exposed in a ring. Each cell is stimulated into activity and divides. This forms a ring of undifferentiated tissue raised up on the surface of the wound. The cells of the ring then divide most actively on the inner aspect, that is, towards the centre. The wound surface bounded by the ring gets smaller and smaller in diameter as the ring itself becomes broader. After some time, the ring closes in at the centre and the wound is covered over by a layer of undifferentiated tissue. Such a layer is called a *callus*, and the wound is said to callus over. The outermost layer of a callus becomes suberized as it is produced, so protection is complete.

When a wound is inflicted on an organ such as a potato tuber, the tissues of which are mainly undifferentiated parenchyma, it is not a cambium which becomes active but the whole outermost layer of undamaged cells. These become again capable of division and quickly form a callus layer over the whole surface.

As a form of recapitulation, the differences between roots and shoots of dicotyledon type may be listed.

ROOT	SHOOT
MORPHOLOGY	
External Surface	
Bears lateral members like itself, branches, only. A limited zone of the surface bears special epidermal hairs characterized by having soft mucilaginous walls and the nucleus in the filament.	Bears leaves in addition to branches. Whole surface may be hairy or not. The hairs usually of more than one cell. One-celled hairs which do occur do not have nucleus in the filament.
Apex	
Primary meristem protected by a special tissue of mucilaginous cells forming a root-cap.	Primary meristem protected by leaves arising at lower levels which turn up to overlap it and form a bud.
ANATOMY	
Narrow pith and wide cortex. Xylem and phloem on alternate radii to give radial bundles. Branches produced endogenously.	Wide pith and narrow cortex. Xylem and phloem on same radii to give collateral bundles. All side members produced exogenously.
MAIN FUNCTION	
Absorption of water and dissolved substances carried on in younger regions only.	Mainly food synthesis carried on in all green parts exposed to light.

THE MONOCOTYLEDON

The description of the monocotyledon type can most easily be accomplished by comparing the differences which exist between it and the dicotyledon. In the first place there is, as has been said, only one leaf in the embryo as compared with two in the dicotyledon.

The Root

In the monocotyledon the main root which develops from the embryonical root of the seed soon dies. The whole of the root system of an adult monocotyledon arises adventitiously from the base of the stem. There is thus little difference between the root system of a normal adult monocotyledon and that of a dicotyledon produced adventitiously under artificial circumstances from a cutting or naturally by some organ used in propagation. The root system of a monocotyledon then has no tap-root, but is described as tufted because it consists of a number of members all of the same size and thickness which originate close together.

The Shoot

In the shoot, except in the leaves, little difference is seen externally between the two types. With very few exceptions the venation of the leaves of a monocotyledon does not form a network. There are a number of main veins all equal in thickness. These follow parallel courses from the base to the apex of the lamina. There are no branches turning and twisting after leaving the parent, though there may be connecting veins which follow a course at right angles to the main veins and so join them together. This provides a method of discrimination between members of the two classes when the leaf is seen in transverse section. The veins of the dicotyledon may be cut transversely, obliquely or longitudinally, depending on how they run in the plane of the cut. In a true transverse section of a monocotyledon all main bundles will be cut transversely and appear practically equidistant one from the other.

The Anatomy of the Monocotyledon Type

A number of differences exist in the anatomy of the two types, though the same elements are used in forming the tissues and tissue systems. For example, there are a greater number of

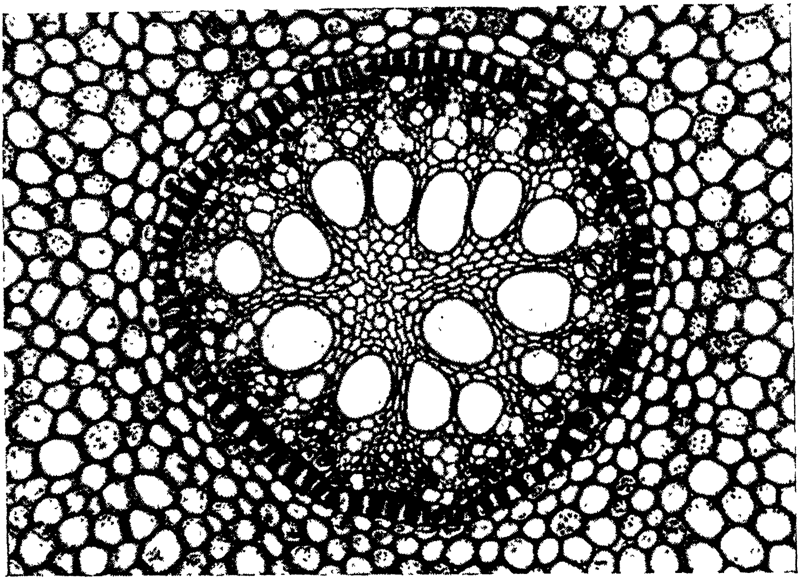


FIG. 25

T.S. Monocotyledon Root to show stile and endodermis. The bundles are radial as in the dicotyledon root, but here there is a larger number. Note the well-developed endodermis

bundles in the axis. A monocotyledon root will show about ten bundles as compared with the four or five primary units of the dicotyledon.

In the root the bundles are arranged in a ring just as in a dicotyledon. In the stem, however, they appear scattered all over the transverse section. In the monocotyledon stem there is no pith, pericycle, or cortex as seen so definitely in the dicotyledon. The bundles are said to be embedded in a general ground tissue. The ground tissue is parenchyma. Usually the bundles nearest to the exterior of the stem are the largest, and are often well supplied with sclerenchyma. There is often a band of sclerenchyma in the ground tissue just below the epidermis. This modification assists in taking the strains caused by the shoot system swaying in the wind.

Apart from a few tree-like members of the lily family, there is no cambial ring in the axis of a monocotyledon. The bundles are not open for further development; they are *closed bundles*, and secondary thickening is not possible. The primary meristem of the apex has to provide for the full thickness the stems and

roots ever attain. Monocotyledon stems, therefore, are usually of small girth compared with their length, and of uniform diameter all the way up, *e.g.* wheat straw.

A form of cambium does appear in the nodes of some aerial stems of monocotyledons. The grasses, for example, possess such an *intercalary meristem.* It remains quiescent until the upright stem is forced into the horizontal position. When this happens, as when corn crops lodge, the cambium in the node adds to the length of the tissues on the lower side. This causes the stem to form an angle or knee at the node, and so turn upwards. Apart from these differences the anatomy of the axes is similar.

The Monocotyledon Leaf

In the leaf the venation differs from that seen in the dicotyledon, and as many monocotyledonous leaves are bifacial they have palisade under both the surfaces, though in these cases the columnar shape of the cells is not well marked.

The epidermal tissues of the two types differ to some degree. In surface preparation the ordinary epidermal cells of a monocotyledon usually do not appear round with sinuous outline, but are always much longer than broad. The long axis of each cell is parallel with the long axis of the leaf and with the course of its main veins. The outline may be sinuous, but the pattern always suggests brick or cobble rather than crazy-paving. There are no intercellular spaces amongst these cells, and none contains chlorophyll. As in the dicotyledon, apart from the stomata, the epidermis presents a continuous colourless layer one cell deep. The stomata in dicotyledons and in monocotyledons (apart from the grasses and sedges) are identical in appearance and mode of action.

The Stomata of Grasses and Sedges

In the grasses and sedges, all of which are monocotyledons, the stomatal mechanism presents one distinctive feature. In surface preparation the guard-cells are not crescentic in shape, but each resembles more a dumb-bell. The two which form the stoma are fastened together at the dilated ends. Associated with the guard-cells are two subsidiary cells which fill in the space lying between the guard-cell and the next adjacent epidermal cells. The pore is formed in the space left by the waists of the dumb-bells, and when open is shaped like a hexagonal slit. The

long axis of the stoma is in line parallel with the morphological axis of the leaf, and the course followed by the veins. In these (grass and sedge) stomata the mechanism of opening and closing does not depend on alterations in the curvature of the guard-cells, but in alteration of the volume of the dilated ends. With increased water intake the heads only of each cell swell; the waists because of their thicks walls remain at the same diameter. The swelling of the ends carries the waists farther apart and the slit widens. Conversely, shrinkage of the ends brings the waists together and the slit tends to close. Seen in a vertical section transverse to the long axis of the stoma, the appearance of the individual cell varies with the point at which the cut passed through. If the heads have been cut the guard-cells are seen as quite large, round in outline, and with very thin walls. If the waists have been cut the cells appear comparatively small and round, but with very thick walls. The difference in wall thickness in the two parts conditions the difference in ability to expand.

DIFFERENCES IN THE VEGETATIVE STRUCTURE BETWEEN THE MONOCOTYLEDON AND THE DICOTYLEDON

Monocotyledon	Dicotyledon
Root Morphology	
Adult system adventitious in origin and tufted in habit.	Adult system a main branched tap-root developed from the seed.
Shoot Morphology	
Stems tend to be the same diameter from ground level to near apex.	Stems tend to be thicker at lower levels and thinner at higher levels.
Root Anatomy	
About ten bundles present. Bundles closed.	Four or five primary bundles present. Bundles open.
Stem Anatomy	
Bundles many and immersed in ground tissue. Bundles closed.	Primary bundles arranged in a ring round a definite medulla. Bundles open.
Leaf Anatomy	
Parallel venation.	Reticulate venation.
Leaves often bifacial with palisade on both upper and lower aspects.	Leaves rarely bifacial, and showing differences between tissues of upper and lower aspects.
Epidermal cells longer than broad. Sometimes sinuous in outline.	Epidermal cells isodiametric (rounded). Sinuous outline.
Stoma (in grasses and sedges) with dumb-bell-shaped guard-cells and hexagonal slit-like pore.	Stoma of two crescent-shaped guard-cells and pore an ellipse.

BOOKS FOR FURTHER READING

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CHAPTER IV

MODIFICATIONS OF THE STANDARD TYPES

MODIFICATIONS of outward form are the result of plants having varied in structure from time to time during the long period of their evolution. The modifications which confer some benefit on the plant in its competition with contemporaries tend to persist. The variation, in some cases, has rendered the plant possessing it more valuable to man. Plants of this type are valued as crop plants or *cultigens*. In other cases the plants are not of use to man, and because of their superior ability to compete and survive may oust or weaken the desired crop plant. These are regarded as bad weeds.

CLIMBING PLANTS

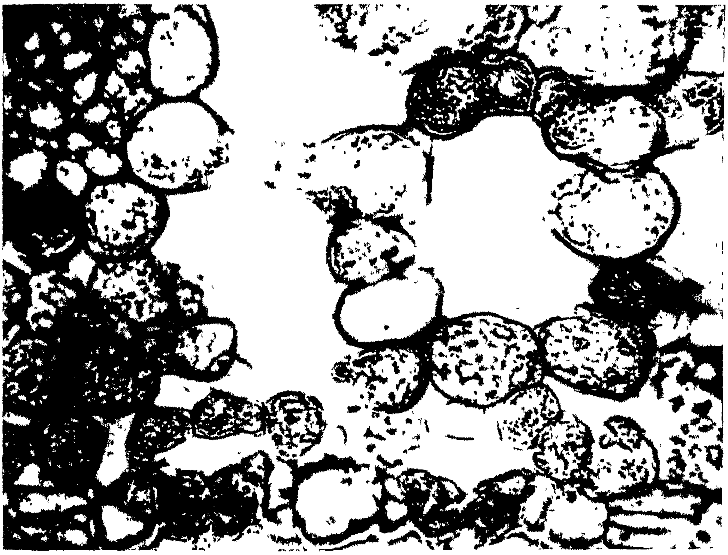
Looking first, then, at the shoot system of the plant, perhaps the simplest set of modifications which have evolved are those designed to help the plant to climb. Light is an essential to all green plants, and those which are left behind in the race upward toward the light may perish or are certainly prejudiced in the struggle for survival. A plant which is slow-growing in its youth or of dwarf habit as an adult, unless it lives in a reasonably open situation not associated with tall competitors, may be smothered.

A fast-growing plant, however, rarely has the necessary reserve of food to form substantial tissues, and its body tends to become weak and straggle.

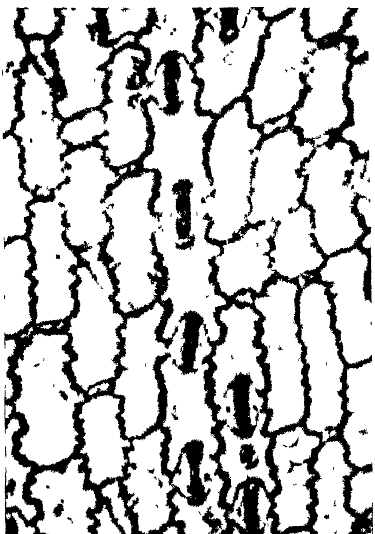
Tendrils

The field and garden pea provide a good example of this straggly growth and also of the tendril, a well-known example of an aid to climbing. In the pea the tendril is a modified leaflet, the terminal one of the compound leaf. A tendril may be a modified branch stem, as in the passion-flower, or a modified main axis, as in the vine.

No matter what the origin the mechanism is always the same. The tendril is thin and whiplike, usually somewhat curved. The concave aspect is sensitive to touch, and reacts when stimulated by contact with a rough twig or similar object. The stimulation must be definite; splashing with water or contact with very



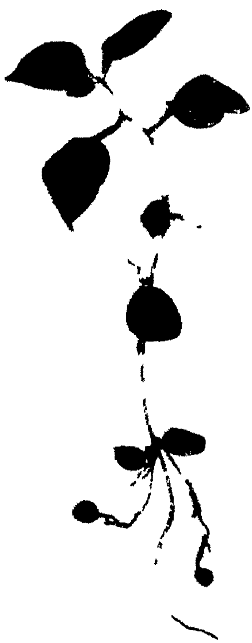
T.S. blade : Two stomata are seen in lower epidermis



Surface preparation. Note the shapes of cells and compare with Plates 12 and 14

PLATE 16

Lucerne : A stool-forming plant



A Potato Seedling

The germination is epigeal. The buds in the axil of the cotyledons form branches which grow downwards and enter the soil. There they form the first small tubers

(See page 86)

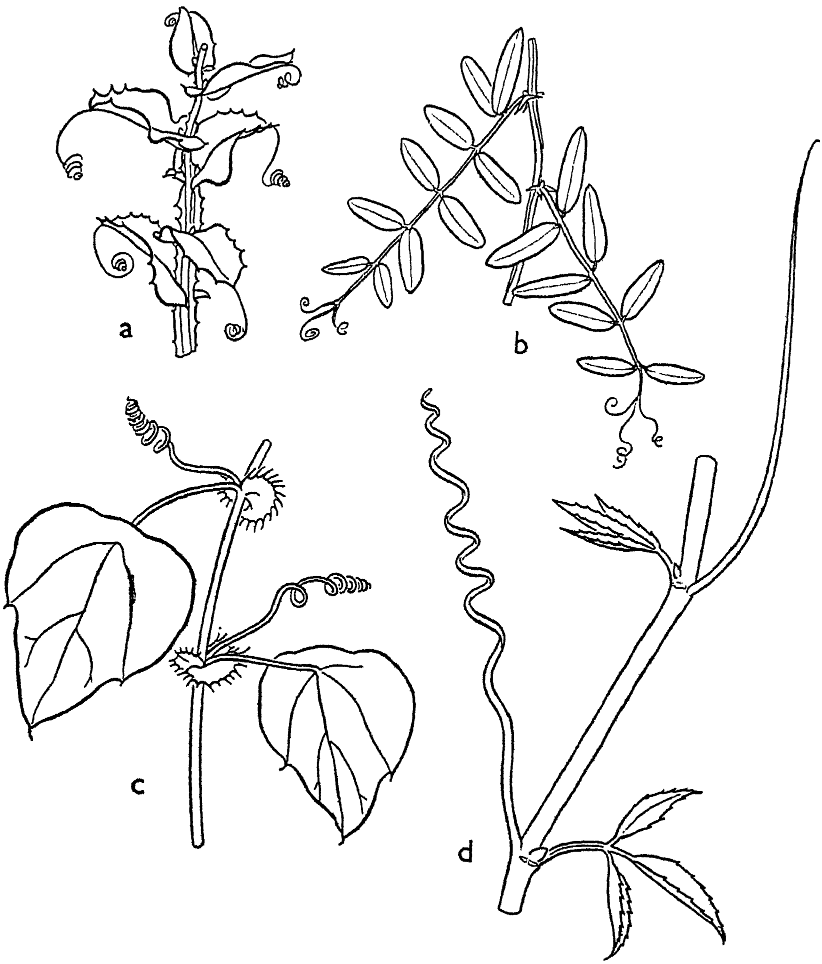


FIG. 26

Tendrils: These may be modifications of (*a*) leaf tip, (*b*) leaflets, (*c*) branch shoots, (*d*) main leader. In (*d*) the branch in the axil of the leaf takes over the "leadership"

smooth surface has no effect. Given, however, that the stimulus is appropriate, the tendril rapidly responds by twining round the object and so gripping it tightly. The portion of tendril between its grip and the base often curls into a helix, and so pulls the plant in towards the support. Any plant supplied with tendrils can straggle up amongst the general growth, and, by their prehensile action, hold on and maintain its position. One position attained,

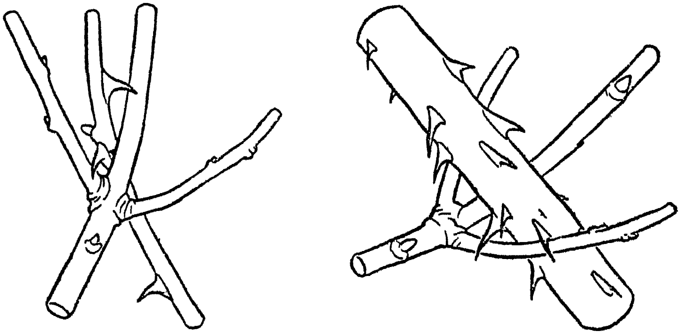


FIG. 27
The recurved prickles of rose (*a*) and bramble (*b*) act as " aerial " anchors

the shoot proceeding upwards produces more tendrils, and so the " hand-over-hand " process is continued.

Another form of straggling climber is seen in such a plant as the bramble or wild rose. The somewhat woody main axis straggles up through its competitors. The downwardly curved grapple-like hooks or prickles produced on the epidermis prevent the long whippy stem from slipping back.

Twiners

A climber of entirely different type possesses a stem axis which though weak remains erect for a while and swings so that the growing tip sways in a series of irregular circles. Should the swinging stem collide with a twig or upright support it continues the motion as it grows, and so twines round and round the support. Such plants are often bad weeds. When they grow in corn they first shade the crop plant, and then by their weight tend to bear it down and cause lodging. Should the corn plant succeed in supporting its own weight plus the weight of the weed, a further disability ensues, for the extra green leaves in the sheaves at harvest add to the difficulties of getting the crop dry enough for the stack. Field convolvulus or black bindweed is an example of this type.

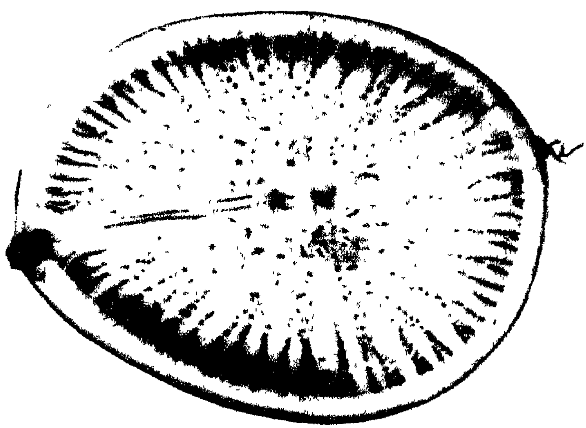
The Twiner Parasite

It will be seen that such a " twiner," pulling itself tightly round a soft stem, might easily sink into the underlying tissue. An extremely close and intimate contact is then established between

Longitudinal section of a potato tuber (lignified tissue stained red)

The point of attachment (by way of the rhizome) to the parent plant is seen at the base of each section. The terminal bud (eye) is seen at the top. The bud in the left-hand section is in the dormant winter condition while that of the right-hand specimen has already sprouted. The vascular bundle is seen running from the base to the apex and going out to supply lateral buds on the way. The main bulk of the potato tuber is pith or medulla

T.S. of " bulb " of kohl rabi (lignified tissue stained red)
The cambium lies between the green zone and the ring of vascular bundles. The main body of this stem is pith. The pith is traversed by small " wandering " vessels, a condition not uncommon in this and related plants



T.S. of turnip or swede (lignified tissue stained red)
The main bulk of this structure is weakly lignified xylem produced by the cambium

the two plants. Over evolutionary time some twiners have taken advantage of this. They now produce on the twining stem structures analagous to, and possibly homologous with, adventitious roots. These strike down into the tissues of the bearer plant and suck out food. A number of the robber, or parasite plants, which steal from their " hosts " have no doubt developed in this way. We see such a case in dodder (*Cuscuta*). In this close relative of the ordinary convolvulus, the sucker-organ or haustorium is very highly specialized. It first consists of an adhesive disc which fixes the parasite on to the surface of the host. Later, a tuft of elongated hair-like cells fans out into the tissues below. These cells may acquire all the characteristics of a conducting tract and make close contact with the elements of the conducting system of the host, drawing water from the vessels and true food from the sieve-tubes. Dodder has gone so far in the direction of parasitism that it now no longer produces any true roots or leaves of its own, and there is no green colour. The adult plant of dodder consists only of its living stem with haustoria and very many flowers.

Climbing Habit—Summary

Summing up, it may be said that support can be got in a number of ways. Whenever these supports occur, they are associated with weak stem and straggling habit. No plant is rendered a good crop plant by reason of its climbing capabilities alone. Those that are valuable for other reasons do quite well without support when grown alone in pure sand and so away from competition. Many climbers are bad weeds by reason of their ability to weigh down or otherwise incommode crop plants.

Annuals, Biennials, and Perennials

Another class of modification results from the fact that the length of the season during which a plant may grow successfully is often strictly limited. The cold of winter in higher latitudes means for the plant slowing down or cessation of growth, or even death. In dry climates, the onset of summer drought may put a period to plant activity.

Many plants develop from seed so quickly as to flower and seed during such a short growing season. These plants which complete the whole life cycle in one growing season are known as annuals.

It is advantageous to a plant when one growing season can be utilized for the production of food which is stored while the plant hibernates over the " dead " period. The store accumulated in one year is used in the following favourable season for the copious production of flowers and seeds. Such a plant taking two years to complete its life cycle is a biennial. The biennial habit imposes the necessity for the modification of the plant body or part of it to provide a storage organ to hold the food accumulated in the first year.

Finally, plants capable of storing food year after year and consuming the stores as required gain a perennial life for the plant body and so attain the perennial habit.

Food Storage and Propagation

Often along with the development of storage organs have come developments for the production of some organ which when broken off from the " parent " is capable of forming a whole plant.

Such breaking up of the plant to produce new units is known as *vegetative propagation* or simply *propagation*. The process is distinct from reproduction in that no sex-mechanism is involved. It is the vegetative phase only of the plant that takes part. The point of interest at the moment is that where a mechanism for conferring bienniality or perenniality has developed, it is often accompanied by a mechanism for vegetative propagation.

Stool Formation

A simple case is seen in many perennial herbs ; that is, plants which live for an indefinite number of years but which lose their above-ground stems at the end of each growing period. In these, the new growth comes each year from lateral buds at or below soil level and borne on the persistent bases of the old stems. As the years follow one another, there is built up a larger and larger cushion-like mass or *stool* made up of old stem bases bearing buds on their outward aspect towards the periphery of the clump. A certain amount of reserve accumulates in the tissues of the stool and masses of adventitious roots are present. A number of crop plants, *e.g.* lucerne and hops, have this type of perenniality-conferring mechanism. In nature this is not very effective as a method of spread or of propagation. After a period of years as

The Cabbage is a terminal bud
(*Photo : Sutton and Sons Ltd.*)

Brussels Sprouts are lateral buds
(*Photo : Sutton and Sons Ltd.*)

MARROW-STEM KALE
(*Photo : Sutton and Sons Ltd.*)

KOHL RABI
Here the swelling of the stem seen in Marrow-stem Kale is carried to an extreme. These two plants are closely related
(*Photo : Sutton and Sons Ltd.*)

an old undisturbed stool all the young active growth is at the periphery, and forms a ring inside of which the old structures weaken or die. In this sense the plant may be said to spread, but if the stools are broken up and carried to a new situation, either accidentally or deliberately, the mechanism serves excellently.

In other plants where the lateral buds which provide each year's active growth diverge horizontally and outwards instead of straightway rising erect, the rate and amount of spread are increased.

Creeping Plants

In the process of evolution, by extending the growth of the lateral bud farther and farther before it turns up to the erect posture, the mechanism has been considerably improved. The final form of this development is the branch produced at or near ground level which takes a definite horizontal course, with the up-turning delayed indefinitely or until an appreciable distance from the "parent" plant has been covered. In the extreme case the central stool may no longer be formed and the plant is recognized as a true creeper.

Rhizomes, Stolons, and Runners

Sometimes the creeping shoots are *below ground* and simulate roots. These are sometimes called root-stocks, but stems which creep below ground are best known as *rhizomes*. In other cases, the creeping branch proceeds at or above the soil surface, and is then known either as a *stolon* or as a *runner*, depending on its behaviour. Runners, stolons, and rhizomes all produce subsidiary plants at a distance from the "parent," and in this may be said to be alike in practice. As the three mechanisms in competition with other plants are not all equally effective, their mode of action must be understood.

The Runner

A runner is formed when a lateral bud of the original axis developed from seed forms a branch which elongates rapidly above ground. After some time the tip touches the ground and adventitious roots develop from it. A short, stumpy vertical axis is then organized, and so the tip of the branch forms a "daughter"

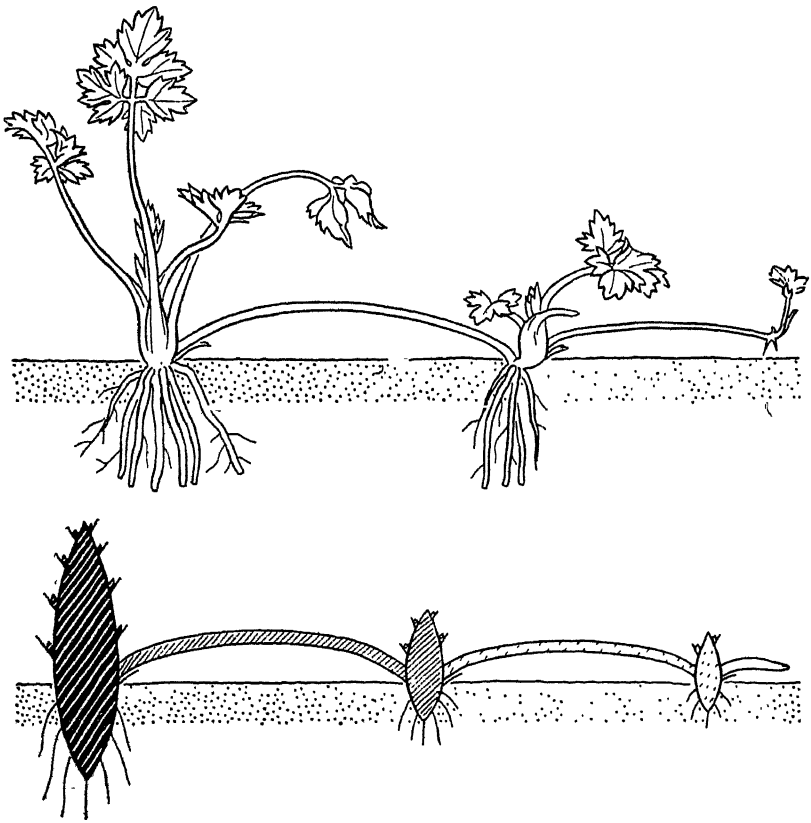


FIG. 28

The Runner

A lateral bud produces each " step " and the terminal of the branch turns down to form the daughter plant. There are few or no nodes between the " parent " and " daughter " plant

plant or *offset.* After some time a lateral bud of this offset repeats the process. Thus a series of over-ground stems connecting " parent " and offsets is made. The stem connection between subsidiary plants dies or is broken, and so a number of free individuals are rapidly produced from one. The storage aspect in this case is not usually important, though the vertical axes may be thickened and used as a storehouse. Offsets from runners are used for production of a crop in the strawberry. Many bad weeds such as buttercup, bramble, etc., are bad because they possess the habit of forming active runners.

Stolons and Rhizomes

Stolons and rhizomes are, as has been said, horizontal stem structures. The point of distinction between them is that the stolon creeps forward *above* the surface of the ground, while the rhizome lies *below* soil level.

The rhizome being below ground is shielded from all light. In the dark, leaves do not expand, and green colour does not develop, hence, in the below-ground stems the leaves are reduced in size to mere scales and are colourless. The stolon, getting more light, usually produces leaves which are more nearly normal.

Monopodia and Sympodia

So long as these differences are remembered, the methods of growth and development of rhizomes and stolons may be described together. There are two types of each. Let each description commence with a seedling plant, though most often in plants of this nature increase is by propagants rather than seedlings.

A lateral bud at the base of the main axis develops into a branch just as in a stool-forming or runner-producing plant. When capable of forming a typical creeping stem, the terminal bud of this branch proceeds for some way producing short internodes and therefore many nodes. In the first of the two possible types, this activity of the terminal in a horizontal direction goes on indefinitely, carrying the stem farther and farther away from the point of origin. Such is indefinite growth, sometimes called monopodial growth and the product a *monopodium.*

In the second of the two types, the leading bud eventually ceases to " lead forward " the creeping branch, and it bends up from the horizontal position to the vertical. In this direction it reaches the upper air and light. Leaves expand and a subsidiary plant develops. The progress of the creeping shoot *as a whole* is not stopped in its course by this behaviour, for a lateral bud immediately behind the bend and on the lower aspect of the stem commences to elongate and proceed in a horizontal plane. In time this new terminal does as its predecessor did and bends up, and again a lateral takes up the lead. The length to which each successive " leader " carries the stem is in a sense limited, hence this is called limited, or definite, or sympodial

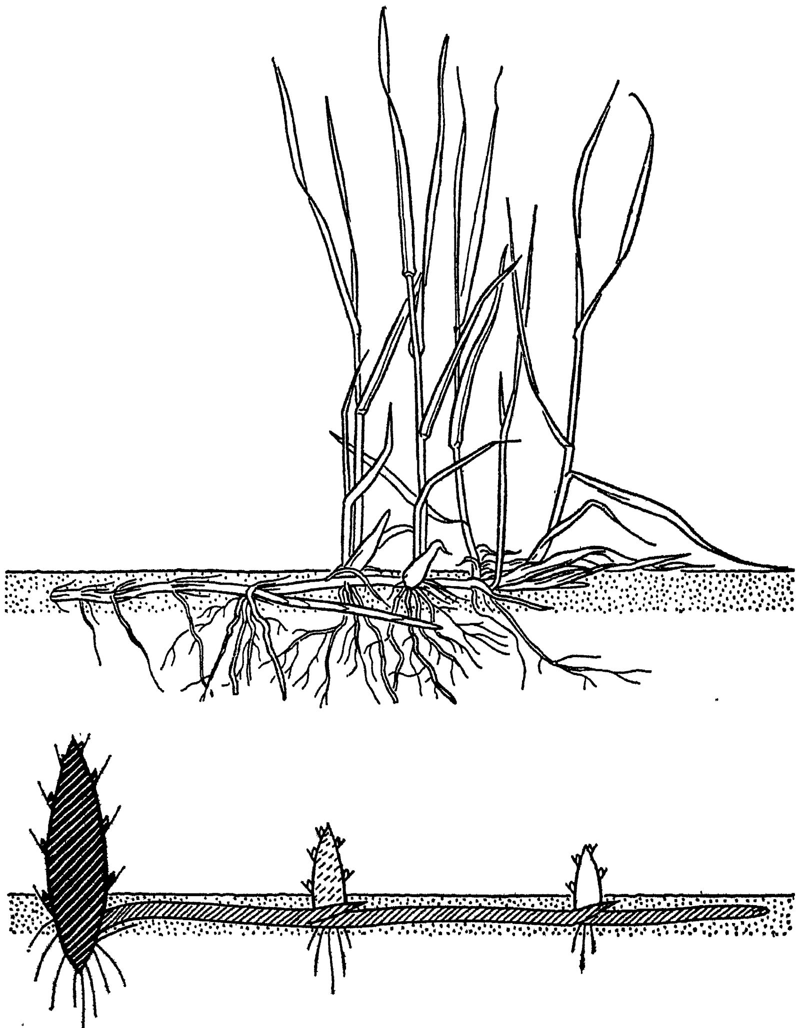


FIG. 29

The monopodium

A lateral bud produces the member, the terminal bud of which continues outwards. Lateral buds produce daughter plants

growth and the product a *sympodium*. The sympodium is really a small advance on the simple stool-forming type. The branch grows farther before turning up. It differs also in that the sympodium branches and rebranches from laterals many times in each growing season, while the stool-former branches but once or only a few

PLATE ROOTS ODIFIED FOR STORAGE

TURNIP

SWEDE

he Swede the terminal bud elongates a little in the first year to form the " neck." In both the swellings are stem to the level of the lowest leaf scar and root up to the highest branch root. The region between is hypocotyl

(*Photos : Sutton and Sons Ltd.*)

The initial material before layering

The material pegged down
(*Photos: East Malling Research Station*)

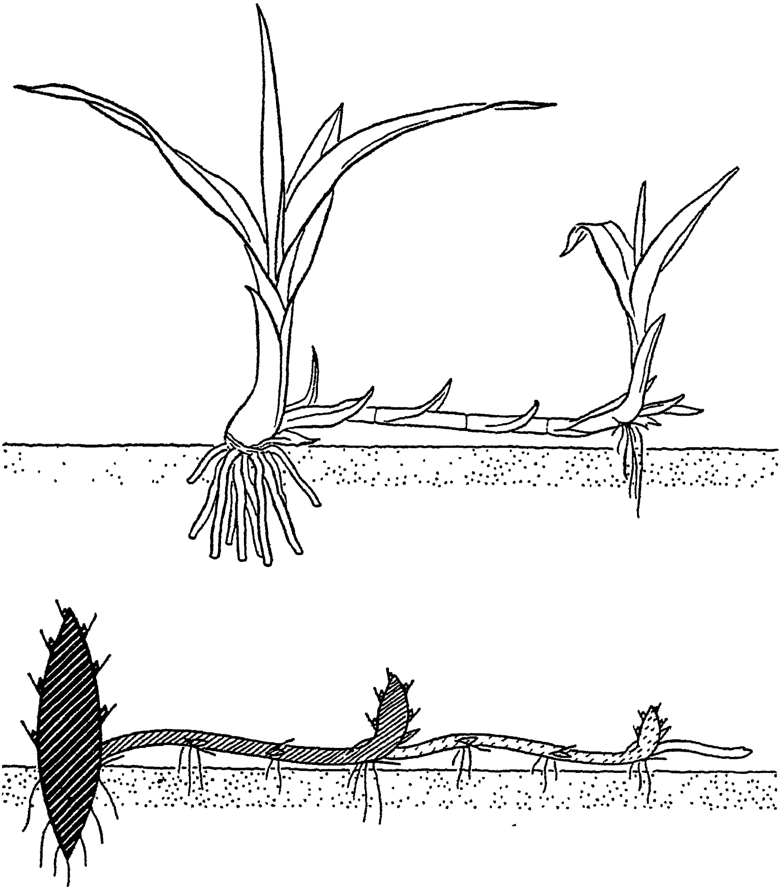


FIG. 30

The sympodium

A lateral bud produces each "step," and the terminal of the "branch" turns up; the root forming nodes at its base common between parent and daughter

times each year from each original stem. The distance travelled by the creeping stem is greater in the sympodium.

These two types of growth, monopodial and sympodial, also occur in the normal stems of the plant (page 24). In these, monopodia are most common, but a sympodium is always formed where the terminal bud (leader) of a shoot changes from its proper job of extension to some other activity. For example, in the vine they form tendrils, and in the lime tree the leading buds die. The stem axes in these two cases are sympodia.

is termed the "rose end," and is the true morphological apex. At the other end (the heel) evidence will be found of the rhizome which originally connected the tuber to the parent plant.

Proof of the Stem Nature of the Potato Tuber

Confirmation that the tubers are stem in nature is got from their anatomy and the following facts. If the green, leafy aerial shoot be cut off the plant before the rhizomes have formed tubers, the ends of the underground stems will curve upwards and rise above the soil to form a leafy shoot. Again, if the aerial stems after a period of normal growth are considerably shaded, the buds in the axils of the expanded leaves will develop into tubers. In many of these aerial tubers the leaves will be partially developed. Finally, the complete proof comes when a potato is grown from a true seed. Germination is epigeal and no part of the stem is below soil level, so no rhizomes develop. Tuberization in a seedling occurs when a branch arises in the axil of each cotyledon and grows downward. The tips of these aerial shoots enter the soil there and form the first tubers.

Other Stem Tubers

The tuber of the artichoke shows its stem nature rather more clearly, for the leaves are more fully developed. In the artichoke only the terminal bud develops on "germination," while on the potato many buds, lateral as well as terminal, develop and produce shoots with equal importance.

THE CORM

All the modifications so far discussed have presented features of branch stems. Other variations leading to storage, propagation, and/or perennation affect more particularly the main axis of the shoot. For example, there is the corm as seen in the garden crocus, which is merely a main stem considerably swollen with food. It is usually situated below soil level. It reaches this position owing to the action of thick roots, which contract strongly, pulling the short stem downwards.

Fig. 33

The stages in the development of a potato from the true seed to formation of first tubers. The cotyledons are carried above ground as seedling leaves

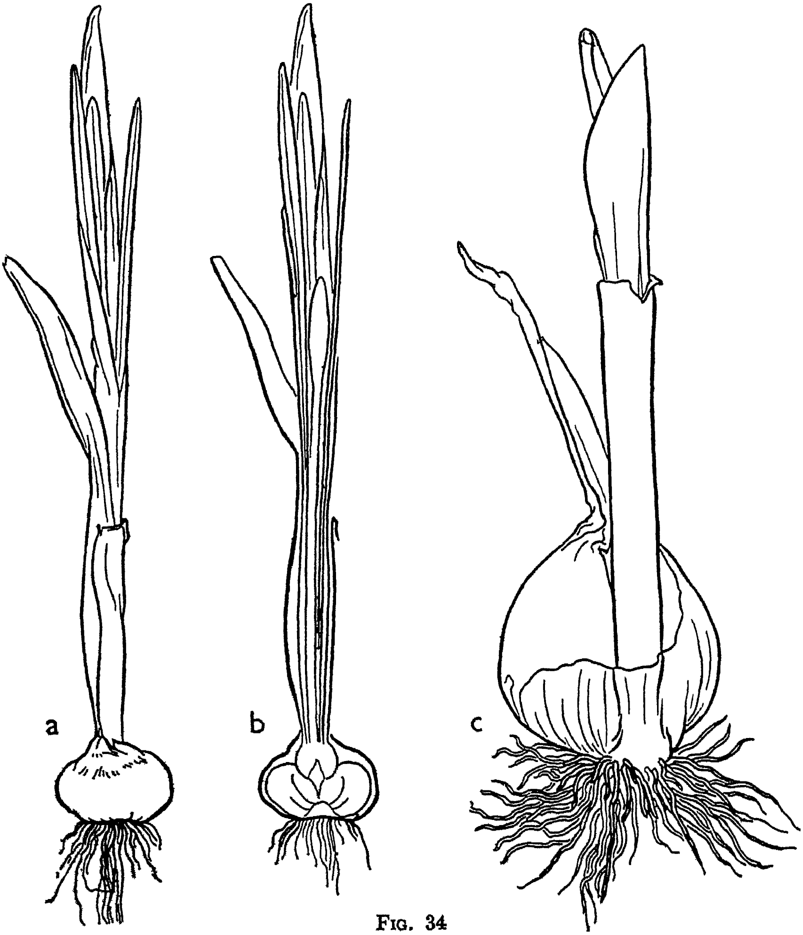


FIG. 34

Crocus corm (a and b) is of one internode invested with scale leaves. Note the new corm is borne at the apex of the old. Meadow saffron corm (c) is similar to crocus, but the new corm is borne laterally

The Development of a Corm-forming Plant

When a plant capable of forming a corm develops from a seed it does not flower in its first year, but the aerial leaves produce food which is deposited in the cortex of the short axis. The first corm is thus formed. This little round body is protected externally by leaves modified to brown scales, and bears at its base a tuft of adventitious roots. In the following spring the axillary buds at the apex of the corm grow up and produce flowers. This

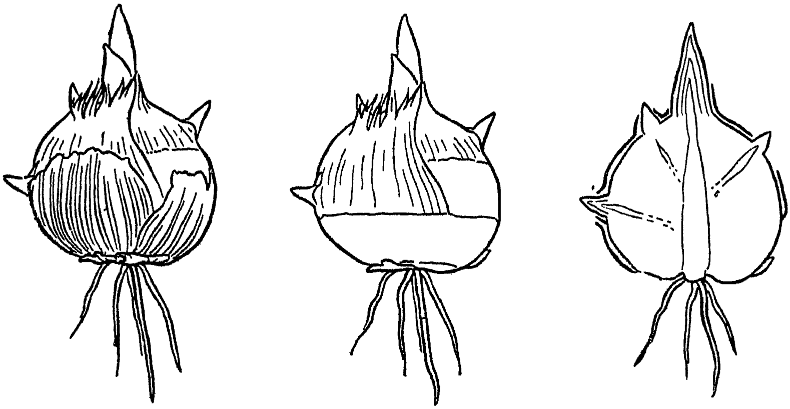


FIG. 35
Montbretia corm is one unit composed of a number of internodes ; buds are produced laterally

drains the food away from the corm, which shrinks completely away. In the summer, after flowering has been completed, the still active leaves continue to form food, which is deposited in the lower internodes of that year's axis, and hence at least one new corm is formed. The new corm is pulled into the soil and there over-winters. In the following spring adventitious roots are produced and the story is repeated.

FIG. 36
Tall oat-grass forms a series of corms, each composed of one internode. If this "string" of corms is broken up each bud grows

The corm type of structure is carried even further in "bulbous" tall oat-grass. Here each internode of the base of the aerial stem becomes filled with food. Each internode is protected by the leaf (with bud in axil), which grows from the node immediately below. The chain of swollen internodes often breaks up into units, each consisting of one swollen internode and one node. Propagation by this means is aggressive and efficient.

In meadow saffron, a poisonous weed of pastures, the bud which forms the aerial shoot in spring is lateral and located near the base of a corm which has over-wintered. The corms for next year therefore arise laterally, and there are usually a number present.

Corm structures are extremely effective for perennation ; and are highly effective for propagation. These facts are well known to anyone who has farmed where tall oatgrass (onion couch) has gained a foothold.

The Bulb

Another case where a vertical stem axis is located below ground is seen in the bulb. The bulb resembles the corm in outward appearance, having a bud at its apex, adventitious roots at its base, and an outer covering of scale leaves. The two bodies differ very considerably in fundamental structure. The corm consists predominately of stem, grossly swollen with food, and in winter condition has all the leaves reduced to thin protective scales. The bulb, on the other hand, consists of a very small stem bearing modified leaves or leaf bases each inordinately swollen with foodstuffs and wrapped round the axis and its growing point.

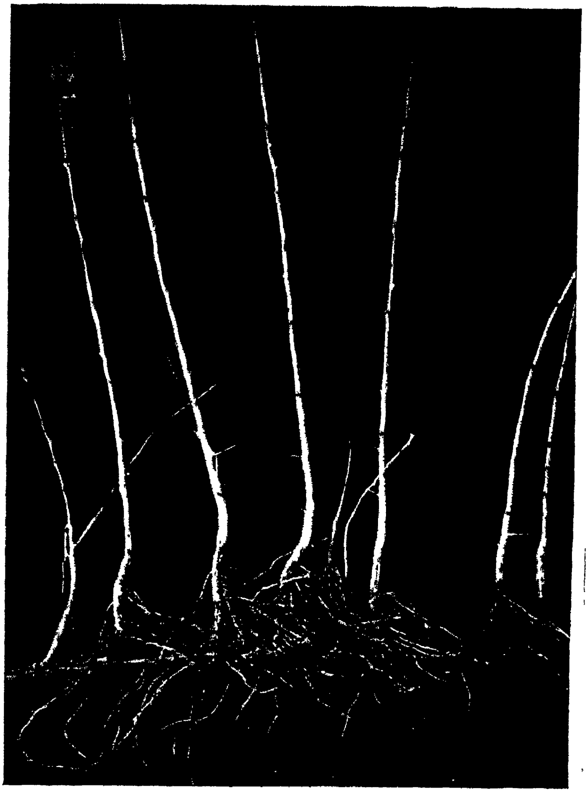
The bulb is therefore not so much a stem as a highly modified bud. The cultivated onion and its weed relations provide perfect examples of this kind of mechanism.

The Development of a Bulbous Plant

In a bulbous plant during the first year from seed the aerial leaves send down food which is stored in their bases. In the autumn the aerial parts of the leaves die down, while the bases of the lower outer ones die and shrivel to form a scaly, dry outer protection. A bulb accordingly in winter consists of a very short vertical axis enveloped in fleshy leaves, and all protected externally by scales. In the next spring the terminal bud of the axis becomes active and flowering takes place ; the bulb shrinks. If the drain on the bulb by flower or seed production is extreme the whole plant dies. Here the bulb confers biennial character ; if, however, the drain is not excessive or is arrested by cutting off the flowers, it will recharge with food during the summer and behave as a perennial. If the terminal bud be damaged after the first spring, lateral buds, one of which is in the axil of every leaf, will become active. These when filled up with food are useful propagants.

In the commercial production of bulbs of, say, hyacinth for the horticultural trade, the terminal bud is damaged by cutting a

PLATE 21 PROPAGATION BY LAYERING



The layer after development

The layered material in "stool beds" for production of stocks in quantity

(*Photos: East Malling Research Station*)

PLATE 22 MARCOTTAGE

Left The plant prepared. (Note the notch on stem just below the leaves)
Right A halved pot assembled round the stem and filled with soil

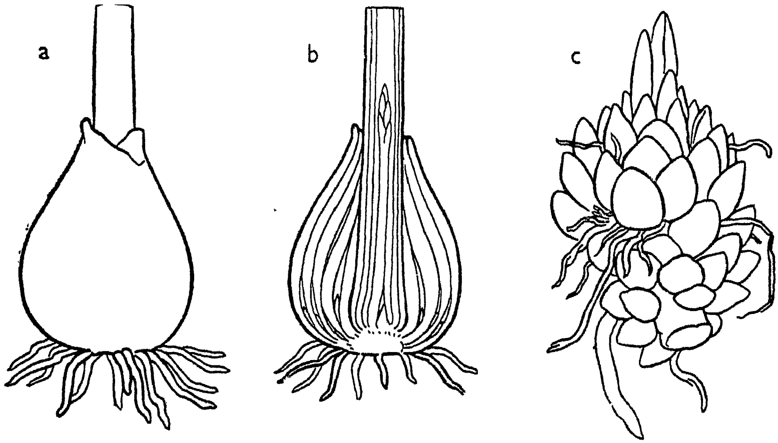


FIG. 37

(a) and (b) Tunicated bulb with layers of overlying leaf structure filled with food ; (c) Scaly bulb with many small leaf structures swollen with food

cone of tissue out from the base of the bulb. A bulb thus mutilated when planted produces ten or twenty small bulbs clustered round the main bulb. These are quite small, and must be grown for a year or two before they are full size.

Such bulbs as that of the onion, where the leaf or its bases extend from base to apex of the structure, the inner ones being completely covered by the outer ones, are called *tunicated* bulbs. Where the leaves or leaf bases are separate and each can be seen as a fat scale as in many of the lilies, the bulb is referred to as a *scaly* bulb. Thus a bulb is rather more than a stem modification, as its main bulk is leaf : it is indeed a modified bud.

Aerial Stems Modified for Food Storage

This leads to consideration of other buds which have a function of storage, etc.

A Terminal Bud : the Cabbage

The easiest example of this class to understand is the cabbage. Here a massive terminal bud with many leaves provides storage for the large quantities of food produced in the first year and consumed by flowering in the second. This bud, of course, has no value in propagation ; it merely confers bienniality.

Lateral Buds: Brussels Sprouts

Another crop plant of similar structure, but where lateral buds are involved and not the terminal, is the brussels sprout.

A Main Stem: Kohl Rabi

An outstanding example of a modified stem conferring bienniality is seen in kohl rabi. Here during the first year of the plant's life practically the whole length of the contracted unbranched main axis of the shoot is involved in producing a large round swollen body. The swelling is due to an enormous proliferation of the central pith, the cells of which are richly supplied with sugar in solution in the sap. In the second year the food is used up in the production of a large amount of flowers, which develop after the terminal bud has elongated.

Kohl rabi, though botanically a stem structure, is usually regarded in practice as a root crop, for there is little apparent difference between the swollen "bulb" of kohl rabi and that of turnip. The one is all stem, the other is almost all root.

Marrow-stem Kale

In marrow-stem kale the stem is not contracted, but the pith is greatly increased, so that the plant occupies a position midway between kohl rabi and the unmodified stem of the annual wild cabbage.

Roots Modified for Storage

Turnip and Swede

In turnip the tissue which is increased is secondary xylem, a product of the wood-cambium. It, in the first year of life, produces a mass of cells which do not modify but remain mainly parenchymatous. The sap of each of these cells becomes charged with sugar. In the second year this food is drawn off to support the mass of flowers which arise in a tall shoot system produced by the elongation of the terminal bud.

Swede shows the same internal organization and behaviour of the root. In morphology the swede "bulb" differs from turnip, for it bears at its apex a short stout length of unmodified stem, the "neck."

Carrot and Parsnip

The roots of carrot and parsnip too are largely xylem, but rather more cortex and phloem enters into their make-up. The wood-cambium is at the outer limits of the so-called core. The wider the cortex, the better the carrot from the culinary point of view. These two roots, too, confer bienniality.

Mangold and Beet

The " roots " or so-called " bulbs " of mangolds and beets, like those of turnip and swede, are practically all root. The make-up of the tissues, however, is quite different from that seen in any

[*Photo: Sutton & Sons Ltd*

FIG. 38

Sugar Beet

This root consists of a small portion of swollen stem at apex, a small portion of hypocotyl, and the major portion true root

other root-crop. In the seedling a normal dicotyledon arrangement is seen. Later, a secondary cambium develops deep in the cortex very much as the cork-cambium has been described as doing in other plants (page 67). Both the original cambial ring and this new one make tissues resulting in xylem inwardly and phloem outwardly. After a period of activity, these two rings become quiescent, and a third cambial ring forms in the cortex again. This ring too for a time produces xylem inwards and phloem outwards and then goes quiescent. This process of initiating secondary cambiums goes on until some five to seven complete rings have formed. Thus, in following a radius outwards from the central medulla, alternate bands consisting of xylem-cambium-phloem are passed. There is usually a band of parenchymous tissue left between the phloem of one ring and the xylem of the next.

Phloem is the tissue which carries sugar down from the shoot for storage. The sieve tubes therefore of all the elements of the root are richest in sugar. Movement of sugar from the tubes to the parenchyma and other tissues is by diffusion and therefore slow. The high concentration of sugar seen in the phloem falls progressively as the distance out from that tissue increases. The inter-ring parenchyma farthest from the sieve tubes has therefore the lowest concentration of sugar in the root. Hence a beet with many rings close together has a higher sugar content than a root with few rings and much parenchyma between. This root storage, as in turnip and swede, confers bienniality on mangold and beet.

Few other root modifications are significant in agriculture, though the root tubers seen in the lesser celandine may be mentioned. In this plant, adventitious roots rise on the base of the stem, each just below a bud. These roots swell up with food. When an adventitious root is broken off, the bud comes away with it, and the unit so formed serves for perennation and propagation.

BOOK FOR FURTHER READING

Fritsch, F. E. and Salisbury, E. J. *Plant Form and Function* (G. Bell & Sons, Ltd., 1943)

PLATE 23 PINEAPPLE

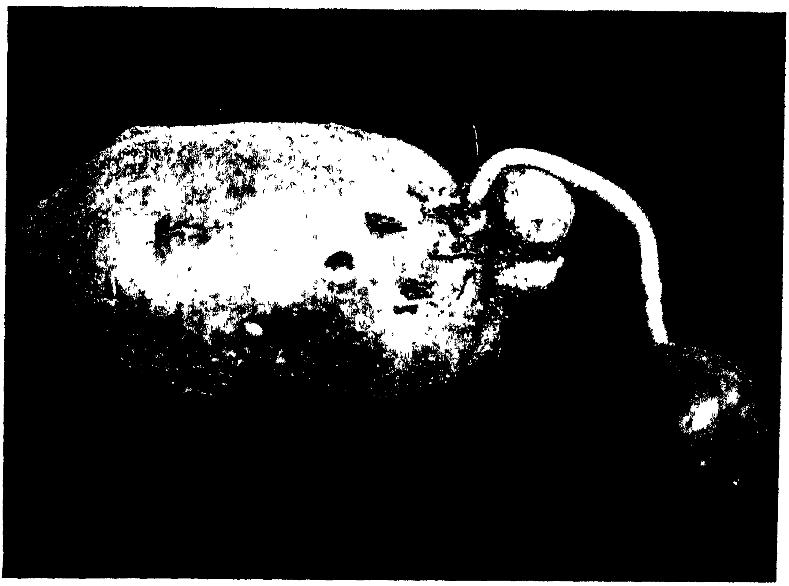
The side shoot " suckers " arising on the main stem below and the " crown '
at the apex of the multiple fruit are used to propagate this crop
(Photo : Hawaiian Pineapple Company, Honolulu)

PLATE 24 SISAL CROP

Upper left A plant showing suckers at the base
Lower left Harvesting the crop

Upper right Bulbils from an aerial stem ready for planting
Lower right Fibre drying after extraction

PLATE 25 SECOND GROWTH IN POTATO

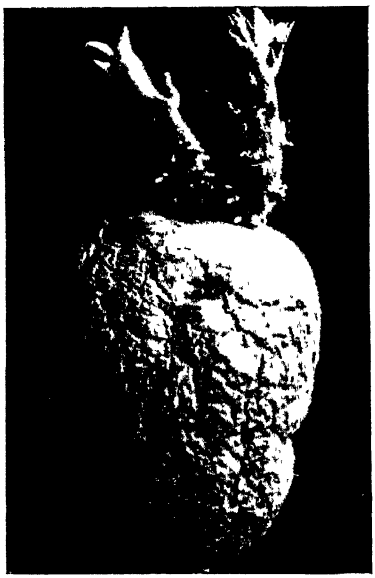


A potato crop checked by dry weather prior to harvest may be mature but not yet dormant. If good growing conditions then occur, the tubers may become active to form second growths

PLATE 26 PROPAGATION : HOPS AND POTATO

Collecting and preparing Hop sets
(*Photograph : Farmer* and *Stock Breeder*)

Potato set sprouted in dark



Potato set sprouted in light

Chapter V

MODIFICATION OF STANDARD TYPES AFFECTING VEGETATIVE PROPAGATION

The studies in morphology and anatomy completed in the previous chapters have a number of direct applications to practice. Their chief uses arise in understanding and exploiting the functioning of the plant which is to be explained in the next section. Many of the direct uses attach to weed eradication and control, for an understanding of methods of natural propagation is necessary for effective action. These and other aspects connected with clean farming form a united whole which will be treated later in a separate section. In this chapter those aspects of form and structure which are effective in propagation and used in the actual production of a crop will be illustrated.

In the temperate regions crop production by vegetative means is restricted to comparatively few cases. Possibly this arises from the relatively high costs involved in collecting, preparing, and planting the propagant compared with seed harvesting and sowing. Vegetative methods are more commonly employed in tropical countries, possibly because vegetative growth tends to be more exuberant there, or because labour costs are lower. Belief in these views is reinforced when it is remembered that the marketed products of horticulture usually bring higher returns than those of agriculture; and in temperate regions vegetative propagation is more popular in the nursery and fruit trades than in farming.

The Advantages of Propagation

In agriculture use of propagation is almost confined to cases where normal seed is not freely produced, not easily harvested, or cannot be relied upon to develop quickly into a uniform, satisfactory crop. Propagation is usually reliable, and the plants produced uniform in character and similar to the plant which bore the propagant. The possible advantages may be summed up as follows: (1) A crop species which does not produce seed or whose seed for any reason is unreliable can be increased with ease. (2) The crop produced from propagants is uniform in character and repeats exactly the good points found in the "parent." (3) The propagant, being composed of adult tissues

and carrying more food than a seed, does not have to pass through all the phases of embryonical development and therefore becomes established in the soil more swiftly and reliably than a seedling. Because of this speed and reliability advantage can be taken of a growing period curtailed at either end by climatic factors such as frost or drought. (4) In many cases a crop raised by vegetative propagation gives a higher yield than would one raised from seed.

Ratooning

Crop production by simple methods approaching propagation in character may be mentioned here. This is seen in a subject like cotton or sugar-cane, which usually occupies the land for only one growing season. Sometimes after harvest the plants are cut back very severely and buds low down are induced to become active. The second year's crop produced from these buds is called a ratoon crop or the stubble crop. Ratooning may be practised over more than one year. The costs of replanting are saved by this, but the method is falling in popularity because by the second year insect pests and disease have accumulated.

Examples of Crop Production by Propagation

In some crops artificial propagants are used. That is, pieces of a normal unmodified stem are cut off a growing plant and induced by suitable treatment to form adventitious roots.

The Use of Aerial Shoots

Sugar-cane is treated in this way. The plant is a tall growing grass. Each stem (cane) shows very definite nodes, each with a well-developed bud. The leafless cane is cut into short portions, each to include two nodes. These " seeds " are planted horizontally in the soil, and after a time adventitious roots develop. One at least of the buds becomes active and develops into a new aerial shoot. Some growers prefer, as " seed," nodes from the upper region of the cane, others prefer those from lower levels.

Crops of cassava or manioc are usually produced from aerial stems. Portions about eight to ten inches long are partly buried in the soil in an upright position. The buried axillary buds develop. The rhizomes of the plant are occasionally used. The pepper crop is got from cuttings which include the topmost nodes or tips of the vine-like stems.

Layering

Other methods of using unmodified stems are commonly adopted in horticulture. Layering is one of them. This consists in bending down and burying the aerial stem in whole or in part. After a while the buried portion forms adventitious roots along its length or in some cases at the node only. The buds at the nodes too become active and form what may be called sucker shoots. The original branch is then removed from the " parent " and cut into portions each possessing a rooted stem. These are planted. This method has proved useful in subjects the stems of which do not root easily, so that a simple cutting would die before rooting became active. The highly standardized grafting material (stocks) of apples and other tree fruits required to-day are produced in this way.

Marcottage

A variation of layering in marcottage. In this the soil is brought to the stem and not the reverse as in layering. A receptacle containing soil is assembled so as to encircle a suitable aerial stem. In place of soil a large bunch of moist fibre or moss may be bound round the stem. Under the influence of this treatment the stem forms adventitious roots. The rooted portion is then severed from the " parent " and planted out.

Parts of the Aerial Shoot used as Propagants, e.g. Pineapple

Pineapple shows many parts of the shoot system being used to produce a new crop. The leafy tufts removed from the top of the fruits and rejected by the canners are called " crowns." These root easily and provide a cheap and easily handled propagant.

" Slips," small parts of the fruiting stem, root readily, as do stumps, parts of the main axis. The parts usually preferred by growers, however, are " suckers." These are small plants which develop from buds in the axils of leaves arising on the stem just below the fruit. These last are preferred because plants derived from them fruit sooner than those from other parts.

Turning now to the use of more natural agents for vegetative propagation employed in agriculture, an intermediate condition is seen in banana, date palms, etc. In these plants erect sucker shoots arising from the base of the stem, and often already supplied with adventitious roots, are broken off and planted.

Sisal too is a crop sometimes produced from suckers, but here, as an alternative, small aerial structures, bulb-like in nature and called bulbils, are often used. These miniature bulbs occur on the aerial stem and replace flowers.

Propagation of the Hop

The hop is one of the crops of more temperate regions commonly produced by vegetative means. As has been explained, the plant is perennial because it forms a stool from buds on persistent stem bases. The aerial stems produced by these buds and developed anew each year are regarded by some as being short rhizomes which turn into the vertical line early in their development. Some of these must be cut off every year or else in time the stools would encroach on the land between the rows, and intercultivations would be prevented or obstructed. This "pruning" is done in spring. When new land is to be planted these prunings are used as propagants. Each is some four to six inches long and bears a number of buds accompanied by adventitious roots. They may be planted directly into the permanent rows the crop is to occupy, or they may be transferred to temporary (nursery) quarters and the planting in permanent rows carried out in the autumn.

Some high-yielding forms of lucerne which do not set seed freely are sometimes dealt with in this way.

Vegetative Propagation of Pasture Plants

The stolons of such plants as strawberry clover, guinea grass, etc., are often used in establishing pasture. The stolons required in these cases are obtained from an existing patch of the plant. The patch is often one specially maintained and used as a sort of nursery. The stolons are gathered up, roughly cleaned, run through a chaff-cutter, and so cut into lengths. The chaffer is set in such a way that it cannot cut a portion so short as not to include a bud. The chopped-up stolons are broadcast on the land and then covered.

Propagation of the Potato Crop

In the potato the tubers of one year are dug up and stored for planting in the following spring. Individuals about 2 oz. in weight are regarded as "seed size." When large tubers are used

as " sets " there is some danger that too many eyes will be present on each, and too many shoots will develop when they are planted. In this case the " seed " or " sets " are cut into portions. In cutting, care has to be taken to ensure that each portion is not too small, and also that some are not left with too few or no buds. In addition, it must be remembered that the buds of the rose end, particularly those nearest the apex, produce the strongest shoots. In cutting potato sets the knife should pass down the morphological axis—that is, from rose to heel—in such a way that each individual cut-set includes at least one of these better buds.

The actual cutting should be done within a few days of planting time. The cut surfaces of the sets are often dusted over with powdered lime in order to dry them and prevent fungi developing. Under favourable circumstances the cut surface of a potato tuber will callus over, but this cannot be relied upon in practice.

Dormant Tubers

Potato tubers immediately after harvest are often in a dormant condition. They are quite alive, but even under ideal circumstances are incapable of " germination." During a period of storage physiological changes take place in the set which permit active growth of the buds when suitable conditions are supplied. The onset of these physiological changes is sometimes stimulated by exposing the tubers to the vapour of certain chemicals, *e.g.* ethylene chlorohydrin, ethylene dichloride, etc.

Sprouting Potato Sets

Often potato tubers intended for planting are induced to form sprouts prior to being put in the soil. At a temperature a little above 10° C. and in some humidity the " buds " of sets that are not dormant commence activity.

It is desirable that the shoots on sets for planting should be short. In this regard it is not the shoot as a whole that is important, but the length of each internode. The reason for this is that tuber-bearing rhizomes of the crop will develop only from lateral buds on those sprouts which are below the soil level. Hence, other factors being constant, the more nodes of the sprouts which are below soil level after planting the more rhizomes with tubers

there will be. The depth to which the set can be planted is limited by practical considerations. Hence a sprout with many nodes, and therefore buds, but with very short internodes, will provide eventually the maximum number of rhizomes below soil level.

Exposure to light reduces extension of internodes, while dark conditions cause them to lengthen. Hence potato tubers intended for planting should be sprouted in plenty of light.

After the set has been planted the earlier cultivations usually practised on the crop are helpful in combating weeds. Many of them, however, particularly harrowing down of the drills, are most useful, because they permit light to reach the developing sets; and elongation of the internodes is checked. The final earthing-up should cover as many buds as possible.

Organs other than Stems may be used as Propagants

In all the examples of vegetative propagation quoted so far, a portion of shoot system forms adventitious roots, and so regenerates a whole plant. Other organs can be used to regenerate a plant. Roots of some subjects may be induced by special treatment to form adventitious buds. These out-growths are of endogenous origin. The different cases are often of great scientific interest, but have little importance in agricultural practice.

Grafting and Budding

Another method of vegetative propagation is the extensive use of grafting whereby a portion of shoot (the scion) of one plant is caused to grow on a root system (the stock), derived from another. In short, by grafting part of one plant on part of another a composite individual is built up.

The essential point in all the methods by which this may be accomplished is that a cambium of one of the components must come in intimate contact with a similar tissue on the other. When this contact is successfully made organic connection develops between the tissue systems of the two. Many ingenious methods of grafting have been devised to increase the area of contact between meristems.

The scion may be a twig, a single bud, or a sheet of bark including a bud, and the stock may be merely the stump of the shoot or a whole tree.

Compatibility of Grafting Material

There are fine physiological questions involved in grafting. In the first place the two components must be in some degree related to each other. Even between grafts of quite close relationship the union may be abortive. One variety of scion will not " take " on a given stock on which another variety of the same kind does quite well. In the unsuccessful cases the components are said to be incompatible. Finally, different stocks produce in the adult plant different habits of growth, different degrees of longevity, and different fertility or vigour when each is grafted with the same variety of scion. Stock and scion relationships are of great practical importance, especially in regard to fruit trees.

Approach Grafting

Just as there are cuttings which die before they produce roots and have to be treated while still on the parent by layering or marcottage, so there are scions which dry off and fail before they can make organic contact with the stock. These are treated by a method of approach grafting or inarching. When this is to be attempted the two plants involved are grown in close proximity. Shoots of each are wounded in a suitable way, so as to expose meristematic tissue. The two wound surfaces are brought into intimate contact and firmly bound together. After some time, when organic connection has been established between the two, the scion part is severed from its parent and becomes a free component of the new plant.

BOOKS FOR FURTHER READING

Argles, G. K. *A Review of the Literature on Stock and Scion Incompatibility in Fruit Trees* (Imperial Bureau of Fruit Production, East Malling, Technical Communication, No. 9, 1937)

Feilden, G. St. C. *Vegetative Propagation of Tropical and Sub-Tropical Fruits* (Technical Communication, No. 13, Imperial Bureau of Horticultural and Plantation Crops, 1940)

Garner, R. J. *Propagation by Cuttings and Layers* (Technical Communication, No. 14, Imperial Bureau of Horticultural and Plantation Crops, 1944)

Chapter VI

MODIFICATIONS OF STEM, ROOT, AND LEAF, IN THE IDENTIFICATION OF PLANTS

Very often it is the duty of a botanist to identify and name plants. When these are presented as whole specimens in adult condition attention is usually directed to the flower and its parts. Most systems for the identification of plants are based on characteristics of the organs connected with reproduction. The agricultural botanist, however, is often called upon to identify plants in the non-flowering, purely vegetative state : twigs from trees in their winter condition, grasses from a close-grazed sward, or even small parts of plants which have been crushed or ground to form a feeding-stuff. It is not uncommon for partially digested fragments of foodstuffs, extracted from the stomach contents of an animal, to be submitted for identification. This may be very important when deaths of stock are thought to be caused by ingestion of poisonous plants.

The classical methods of identification using characters of the flower are not applicable in any of these cases, and therefore small variations of the vegetative phase characteristic of each plant have been described, and these are used.

Recognition of the Larger Groups

From what has gone before, methods of deciding whether a specimen of stem or root is a monocotyledon or a dicotyledon will readily be deduced. So too a leaf of grass or sedge may be recognized if a stoma is present. Examples will be offered here of different systems applicable to different groups of plants significant in agriculture, and each is capable of defining individual kinds of plants, not just classes or groups.

Identification of Trees and Shrubs in Winter Condition

A number of trees or shrubs come within the purview of the agriculturist. The twigs of those in winter condition bearing neither leaves, flowers, nor fruits, but bare apart from buds, may be sent for identification. The buds, bark, and leaf scars often provide sufficient features for this identification.

TABLE I

TABLE I.—SUMMARY OF CHARACTERS USEFUL IN THE IDENTIFICATION
WINTER CONDITION AND NOT

	NAME	BUDS (Buds sessile except in cases specially noted)			
		Size	Shape	No. of scales	Colour
	BUDS OPPOSITE				
1	Dogwood	not small	longer than broad	2 to 4	grey
2	Common Maple	small	broader than long	several	green-brown
3	Norway Maple	intermediate	ovoid	several	red-brown
4	Ash	large	globose	2–4	black
5	Elder	large	ovoid and open	many loose	reddish olive
6	Sycamore	intermediate	ovoid	several, compact	green; dark tips
7	Spindle tree	intermediate	narrow	several	green, red tips
8	Privet	small	pointed	4–6	green
9	Honeysuckle	intermediate	4-angled	many	green-brown
10	Wayfaring Tree	small	long	2 or none	grey-brown
11	Guelder Rose	not small	oval	1–2	red-brown
12	Horse Chestnut	large	longer than broad	several	red-brown
13	Buckthorn	small	ovate	several	red-brown
	BUDS ALTERNATE IN TWO ROWS				
14	Spanish Chestnut	large	angular	2–3	yellow-green; red-green
15	Lime	intermediate	fat, globose	2–3	grey-brown
16	Beech	long	long and pointed	many > 12	chestnut brown
17	Elm (common)	small	oval, pointed	several	grey

OF THE TWIGS OF SOME COMMON DECIDUOUS TREES WHEN IN ALREADY DESCRIBED IN THE TEXT

BUDS Hair	BARK Colour, etc.	NOTES	
		BUDS OPPOSITE	
hairy	smooth	twig bright red after frost	1
hairy	tawny and corky	stems angular ; opposite scars meet	2
none	smooth, red-brown	milky latex in tissues ; scars ringed so they meet round twig	3
hair	smooth, green-grey	terminal bud > laterals ; stem flat at nodes ; bud scales keeled	4
none	grey-green	bark " gritty " to touch ; broad pith ; sickly smell when crushed	5
none	smooth, grey-brown	scars crescentic but do not meet round twig	6
none	greenish	stems ridged ; sometimes 4-angled	7
none	smooth, dark green	not completely deciduous	8
none	glossy brown	twining stem ; hollow pith ; buds open early	9
stellate hairs	stellate hairs ; grey	flower buds short stalk ; bud scales fall early	10
none	smooth, grey-yellow	the two bud scales are fused	11
marginal hairs	brown	buds gummy, twigs stout	12
none	grey	branches end in thorn ; spur shoots with no thorn ; buds occasionally not quite opposite	13
		BUDS ALTERNATE IN TWO ROWS	
none	brown	bud off centre of scar ; twig ridged	14
none	smooth ; red-yellow	twig axis zigzag	15
on top of scales	dull grey	buds stick out from twig, at angle ; longer than broad	16
hairy	± hairy	there are a number of elms ; this is the common one	17

	NAME	BUDS (Buds sessile except in cases specially noted)			
		Size	Shape	No. of scales	Colour
1	Hornbeam	intermediate	oval, pointed	many	brown
2	Hazel	intermediate	plump and blunt	several	pale brown ; red-green
	BUDS SPIRAL IN MORE THAN TWO ROWS				
3	Alder	intermediate	small clubs	2–3	violet
4	Blackthorn (Sloe)	very small	globose	several	dark brown
5	Hawthorn	minute in pairs	round and pointed	several	red-brown
6	Plane	intermediate	conical	1	grey-red
7	Willow (Crack)	large	oval, pointed	1	yellow
8	,, (White)	small	oval, pointed	1	white
9	,, (Sallow)	inter.	oval, pointed	1	yellow
10	Walnut	large	oval	several	black
11	Mountain Ash (Rowan)	large	triangular	several	black ; dark purple
12	Common Oak	large	blunt and angled	many	grey-brown
13	Aspen	small	conical	several	brown
14	Black Poplar	small	conical	several	yellow-brown
15	Grey Poplar	small	oval	several	grey
16	Birch	small	oval	several	reddish
17	Apple (Crab)	not small	oval ; 3-angled	several	brown
18	Pear (Wild)	not small	oval	several	dark brown
19	Plum (Wild)	intermediate	conical	many	dark brown
20	Wild Cherry (Gean)	large	ovoid ; pointed	several	brown
21	Barberry	small	stumpy	none	red-brown
22	Larch	small	globose	many	brown

Continued

BUDS Hair	BARK Colour, etc.	NOTES	
hairy	rough	buds similar to beech, but appressed to twig	1
hairy	pale brown	male catkins conspicuous ; glandular hairs	2
	BUDS SPIRAL IN MORE THAN TWO ROWS		
waxy bloom	blue-grey	triangular twig ; violet waxy bloom	3
hairy	smooth ; grey-brown	thorns are branch tips ; spurs and terminals ; buds in clusters	4
none	smooth ; grey, purple-green	thorny branch spines	5
none	smooth ; light brown	tubular petiole-base, leaves a ring scar round the bud	6
none	glossy		7
silky	silky hair	These are types from a complex group of many forms	8
smooth	red ; no hair		9
terminals hairy	green-brown, smooth	lateral buds not hairy ; pith chambered	10
tips hairy	maroon to grey		11
hairy	ribbed and ridged grey	twig axis makes irregular changes of direction ; buds in clusters	12
none	shining ; pale brown	twigs glabrous	13
none	yellow ; ribbed	twigs may be hairy or not ; buds sticky	14
cottony	cottony ; ribbed		15
shining and sticky	warty and hairy	twig thin and whiplike ; another form has downy buds	16
hairy	glossy ; red-brown	spur shoots may carry spine	17
hairy	smooth ; yellow-brown	branches often thorny ; on margins of scales	18
hairy	smooth ; red-purple	on margins of scales	19
none	smooth ; blue-brown	bud scales keeled, with mucronate point ; buds aggregated on spurs	20
none	red-grey	1–3 spines below each bud	21
none	rough	twig rough, due to persistent leaf bases ; buds resinous ; cones often present on twigs	22

Arrangement of Buds on Twigs

The bud arrangement is fundamental. The first separation of material can be into two-classes : (*a*) buds in pairs, and (*b*) buds alternate. This second class (*b*) can be split to include on the one hand those twigs where the phyllotaxis is one half, and on the other those with phyllotaxis some fraction smaller than a half.

Characters of the Buds

These three classes can be further sub-divided on the basis of other features. The buds of some trees are sessile, on others they are borne on stalks. Again, some buds are protected by scales, the number of which is constant for a given tree, or the buds may have no protection but remain naked. The various associations of these different features are characteristic of twigs of different kinds. For example, on the black and the red currants the buds are arranged alternately, carried on short stalks, and are protected by a number of scales. They are almost unique in this. The two may be differentiated by other features. The red currant has a grey-coloured bark, which comes off in long scale-like portions. There is no odour from the twig. The bark in black currant is smooth, dark olive-green to black in colour, and the twig, especially when crushed, emits a characteristic smell.

The vast majority of woody plants of the farm, apart from these two, have sessile buds arranged in a spiral. From this a group with "prickles" on the surface of the bark may be isolated. This includes the gooseberry, barberry, wild rose, bramble, and raspberry. The rose, bramble, and rasp have backwardly-curving prickles scattered over the whole surface, while on the gooseberry and barberry the spines are straight and not scattered but inserted below the buds. The bark in gooseberry is greyish, while that of barberry is dark. The buds in barberry are blunt as opposed to the sharp-pointed ones of gooseberry.

The necessary data for "spotting" the twigs likely to be submitted to a botanist in Britain have been here assembled in Table I. All trees which have salient features in common have been grouped together. When a twig is found to possess a group character, another feature used in the table should be looked

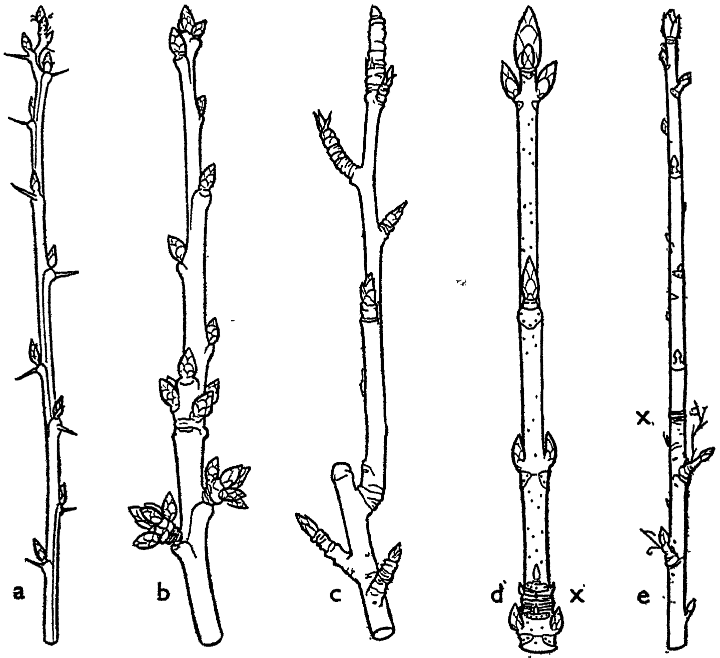


FIG. 39

Some characteristic twigs

(*a*) Gooseberry (*b*) Cherry (*c*) Pear (a lateral bud has here taken the lead)
(*d*) Horsechestnut (*e*) Blackcurrant

The scars shown x are typical of those left by the scales of a terminal bud, and mark the base of one year's growth

for which will differentiate the individual from the other members of its group.

The grouping adopted here is quite arbitrary, and the student is advised to construct other tables bringing the various kinds of twig into different relationships. So, too, plants not included in the table should be identified while in summer condition, and then in the subsequent winter the twigs examined and their salient characters noted.

THE PASTURE PLANTS IN VEGETATIVE CONDITION

The plants of our pastures often have to be identified in the non-flowering condition. These are usually grasses or clovers and their allies. The clovers and all the plants allied to them are dicotyledons, while the grasses and their allies, are monocotyledons.

The bark is separated from the cambium

The prepared scion is inserted

The union is sealed with grafting compound

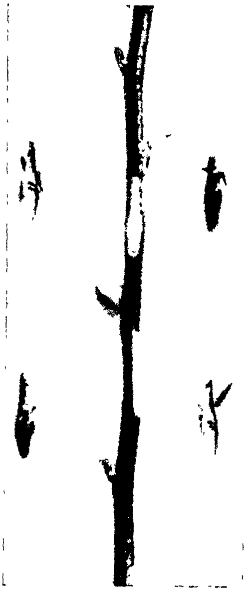
The scions " take " and the tree is refurnished

In this and in all other forms of grafting or budding the important point is that close contact should be made between the cambium of the stock and that of the scion

PLATE 28 STRAP GRAFTING

Left to right A cleft is made in the cut end of a branch of the stock; the scion is inserted so that the cambiums make contact. In time the activity of the cambium of the stock covers over the wound

PLATE 29 BUDDING AND TONGUE GRAFTING



The buds prepared

The stock prepared, the bud inserted and the wound bound up

The scion made to fit on a saddle or tongue of the stock is placed in position and bound up. The fit must be neat. Note twig on right

PLATE 30 EFFECT OF STOCK ON SCION

The same variety of Apple (Bramley) grafted on (*left*) Malling IX Stock and (*right*) Malling XII Stock. Both trees were treated alike and are of the same age

(*Photo : East Malling Research Station*)

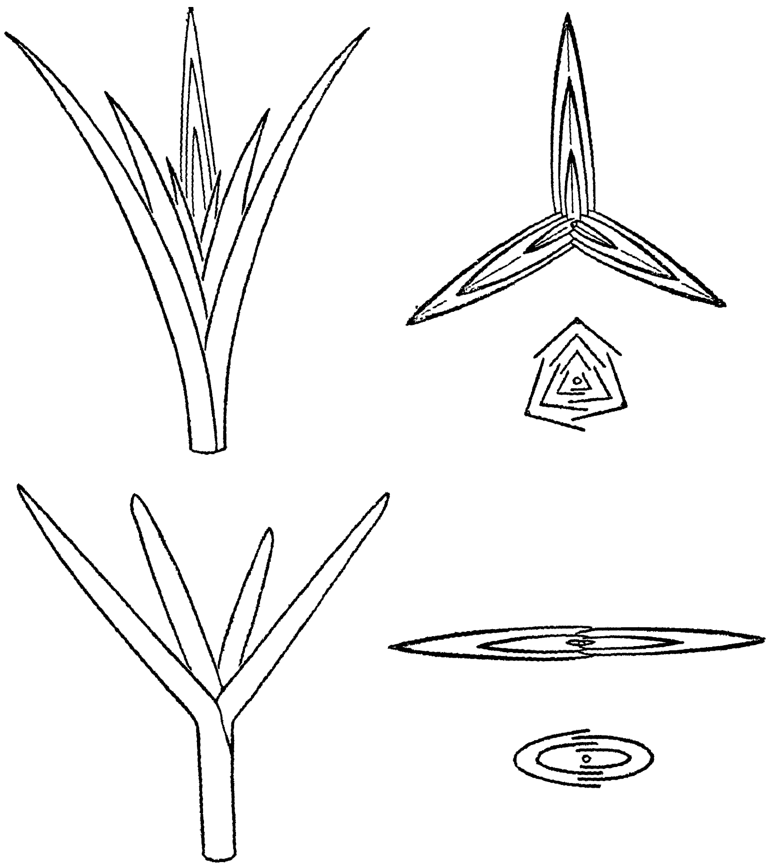


FIG. 40

Sedge and grass—leaf arrangement, seen from the side, from above, and in ground plan

(*above*) Sedge (*below*) Grass

GRASSES AND THEIR ALLIES

Looking at the grasses first, they are readily separated from all other grass-like plants because their phyllotaxis is a half, while that of the non-grasses is one third. A plant found in grassland showing the characteristics of a monocotyledon and phyllotaxis one half, that is, with the leaves alternate in two rows down the stem, will be a grass. Similar-looking plants with the leaves also alternate but in three rows will be sedges or their allies.

Within the grasses, the roots, stems, buds, and leaves all

present features of interest. In order to understand the significance of the various features, some understanding of the biology and structure of the grasses is desirable.

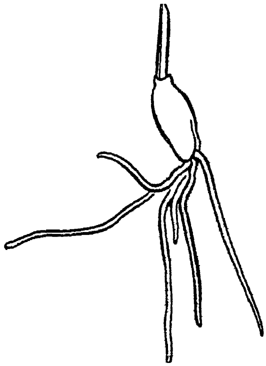


FIG. 41
The seminal roots of barley

The Grass Seedling Root System

Grasses are peculiar in the method of production of their root system. On germination, the "seed" seems to produce more than one main root. More correctly it should be said that the radicle very early forms a number of branches of equal thickness, and these all emerge through the "seed" coverings simultaneously. These are known collectively as the *seminal* root system. The function of the seminal root system is temporary, and is to provide for the supply of the seedling stage only. Later on it dies. If other methods fail, the roots may be useful in identifying seedlings of the cereals. For example, in wheat and oats the number of main seminal roots is three, in rye four, and in barley five or six.

During the period when the seminal roots are active the growing point of the shoot is carried up to the surface of the ground by the rapid elongation of the first internode. The first true node is carried up to soil level irrespective of the depth (within reason) to which the "seed" was planted. This first node is of importance in the subsequent history of the plant.

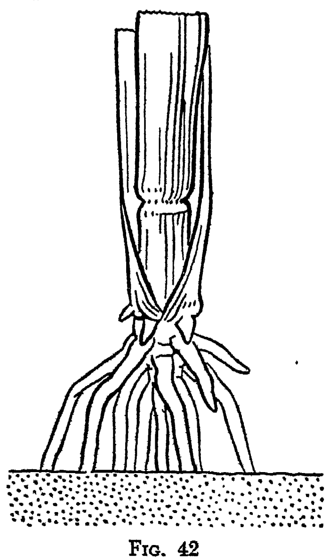


FIG. 42
Strut-roots

The Grass Adult Root System

It is from the first node that the permanent root system develops adventitiously. Thus the permanent root system of grasses always originates at or near the surface of the soil and has then to grow down to lower levels. As it originates at the "crown" it is called the *coronal* root system.

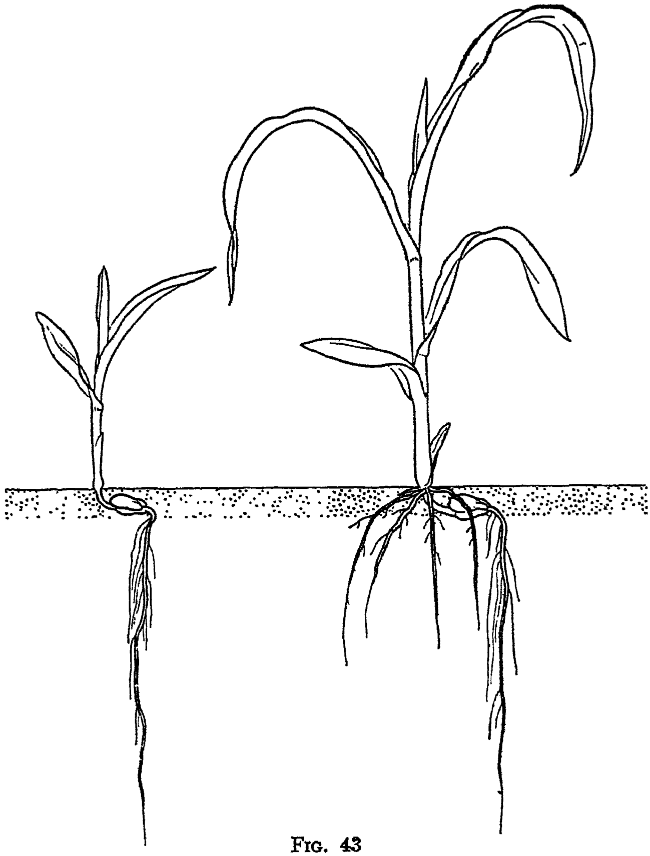


FIG. 43
The root systems of a grass (maize)
Left Young seedling, seminal roots only
Right Older seedling, seminal and coronal systems both present

During the change-over from the seminal to the coronal root system there may be a period of weakness in the plant.

The adult plant later on may produce adventitious roots higher up on the shoot. These act rather as struts or props, and are therefore called strut-roots or prop-roots.

The Shoot of Grasses

When the growing point of the seedling shoot reaches soil level the subsequent internodes remain short, at least for a time. The plant is said to " set " or " sit." The very short axis so constituted is the crown, and from it all buds of primary order originate.

Hence, the branches all originate at or about ground level, very much in the same manner as a "crown" of branches forms at the top of the unbranched trunk in many forest trees.

Tillers and Tillering

When a plant produces branches in a crown at ground level, it is said to tiller, and the branches are called tiller shoots or tillers. The amount of tillering in a grass plant is controlled almost entirely by heritable factors in conjunction with the amount of light reaching the crown. Some varieties tiller more freely than others. More light at the crown results in more tillers, while less light gives fewer branches. In a thickly sown corn crop less light reaches the crown than is the case in a thin crop. Thus, in a thin crop tillering is encouraged, and the crop is said to thicken or tiller-out. In the thickly sown crop, even of a freely tillering variety, branching will be restricted or even inhibited by lack of light. Other factors affect the position, but these two, light and inheritance, are the most important. Later in the history of the plant, usually as a prelude to flowering, the terminal buds of tillers become very active, the branches elongate rapidly, and the plants are said to shoot.

The Grass Culm

The stems produced by grasses when they shoot are long, straight, hollow cylinders of small diameter with the flowering region confined to the part near the apex. Such a stem is called a culm. In some grasses the culm has nodes where leaves are produced, but the bud in the axil of each does not develop. At the culm nodes the hollow stem is filled in and is said to be solid at the nodes. Very few grasses have culms which are solid all along their length, though one well-known example is maize. Tillers which do not shoot and have no flower are said to be vegetative, or barren, or sterile.

Features of Grass Plants used in Identification

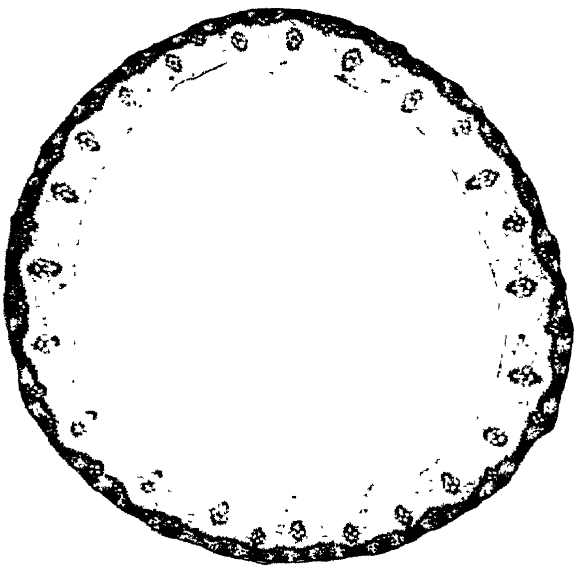
The Root System

Turning now to the characteristics of the non-flowering adult grass plant used in identification, it is seen that, as in most monocotyledons, the roots are all adventitious and have their

PLA'   EFFE'   OF STOCK ON SCION

“ Fertility ” Pear grafted on Quince stock. (*Left to right*) Quince A Quince D Quince E
All trees are six years old
(*Photo : East Malling Research Station*)

Section through a plant of Yorkshire Fog. The sympodial stolons form a loose tuft



Transverse section of a grass culm. The central ground tissue has been absorbed. Note the concentration of bundles and sclerenchyma at the periphery

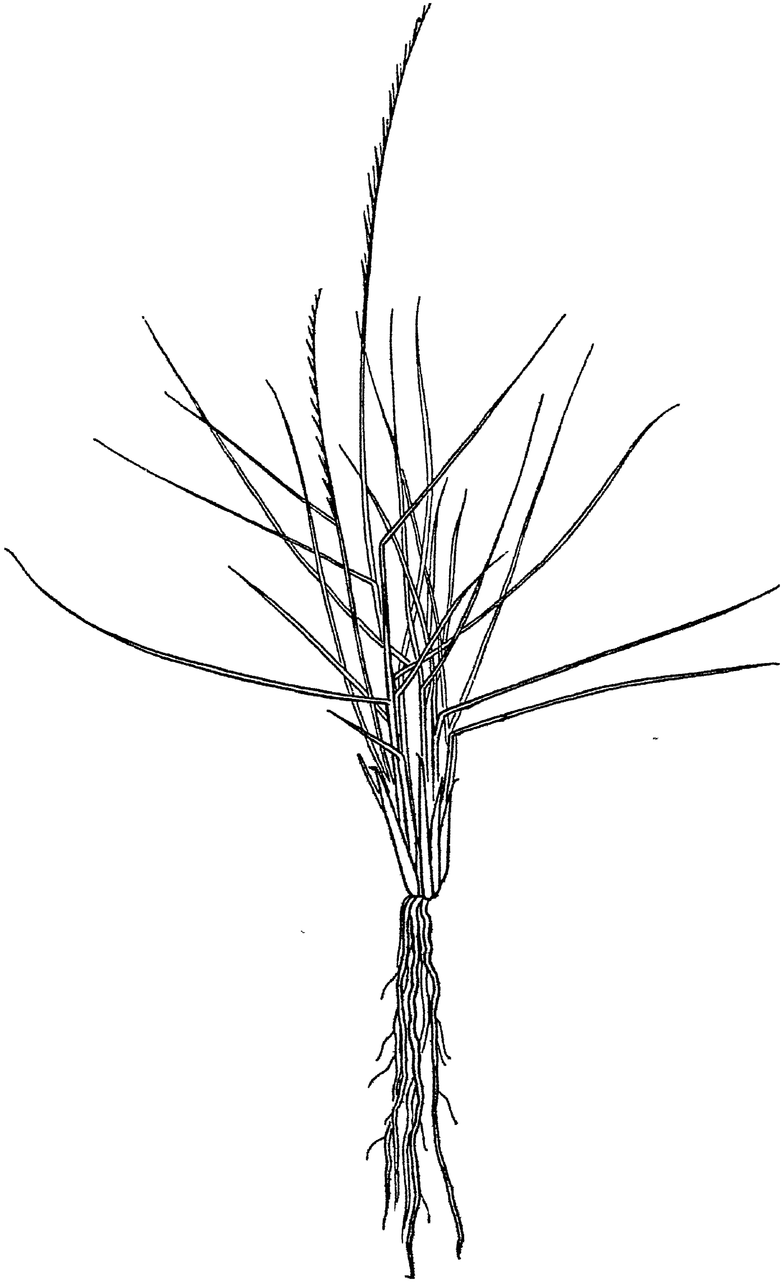


Fig. 44
Plant of moor mat-grass

origin near to the surface of the ground. The root system consists of many members, all of equal though limited thickness. There is no tap-root and the system as a whole is tuft-like. Apart from the seminal system of seedling cereals, roots in grasses provide features for identification of the adult plant in a few cases only. Two of these are moor mat-grass and purple molinia, where the several members of the adult root system are not truly fibrous but thick, and resemble cords. These grasses are said to have cord-like root systems.

The Tillers

The shoot system provides a number of points useful in identification. If the greater proportion of the tillers on a specimen are in the fertile condition, the plant may be assumed to be of annual habit. If on dissection the greater number prove to be purely vegetative, then the plant is probably perennial. Should the actual specimen in hand be of a perennial and more than one year old, then the bases of tillers of previous years' growth will be present and provide additional and conclusive evidence on this point.

Those grasses which shoot to produce tall culms, especially if these carry leaves, add to the hay yield. These are called top-grasses. On the other hand some grasses produce short culms, and the great proportion of the leafage is situated near the ground. These are called bottom grasses.

The Leaf

Except in certain cases to be specifically mentioned, it is the ground leaves which are used in the identification of grasses. The cauline leaves borne on the flowering culm are rarely used in this work.

The ground leaf is the centre about which nearly all points of grass identification turn. If one such leaf is gently pulled away from the stem four parts may be recognized. The blade or lamina is free. The petiole or sheath is seen to encircle or clasp the inner-lying leaves and the stem. Up at the top of the sheath where it joins the blade or lamina a small frill or tongue-like structure will be found. This is an up-folding of the morphological upper epidermis of the sheath, and is called the ligule. The margins of the lamina at the base where it joins the sheath may be prolonged into two small ear-like processes called auricles. The

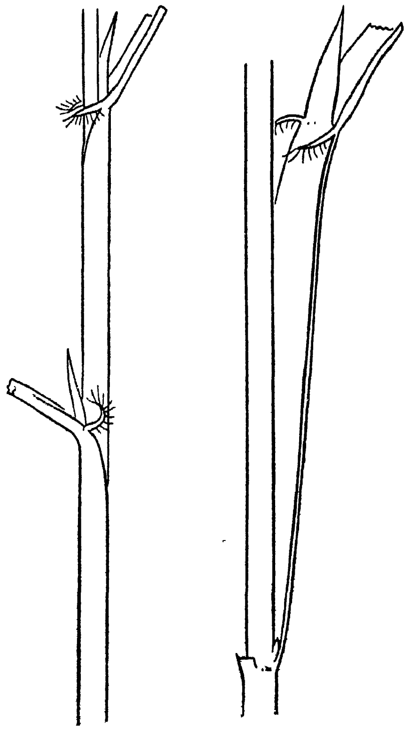


FIG. 45

The parts of a grass leaf (blades cut short)

Left The leaf in natural position

Right Pulled away from stem

From below upwards note bud in axil, sheath or petiole, auricles (hairy), ligule (long and pointed) and blade

grass leaf has always a sheath and a blade, nearly always a ligule, and often a pair of auricles. Variations in the size, shape, and occurrence of these provide many of the characters used to differentiate one kind of grass from another.

Branching and Habit of Growth

The bud which lies in the axil of the leaf down at the base of the sheath provides the next feature of interest. When the bud develops to form a branch it may behave in one of two ways. On the one hand, it may grow vertically upwards, passing between the sheath and the stem. This is called intra-vaginal branching, and results in a tufted habit of growth. On the other hand, the developing bud may proceed horizontally and burst through the leaf sheath. Such a method of development is called extra-vaginal branching, and is seen in all grasses of creeping habit. The creeping tillers from extra-vaginal branching may keep below soil level and so produce rhizomes, or they may lie above the ground as stolons. Some grasses are rhizomatous ; others stoloni-

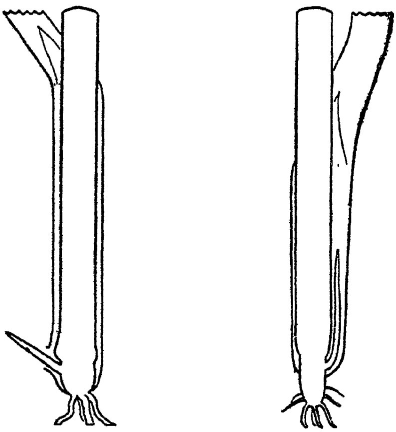


Fig. 46
Development of the grass bud
Left · Extra-vaginal development—creeping habit
Right Intra-vaginal development—tufted habit

ferous. Care should be exercised in using this character for identification, because there is reason to believe that some grasses can be either stoloniferous or rhizomatous, depending on the soil-water level. In wet soil the tillers tend to be stolons, but in drier soil they go deeper and are then described as rhizomes. The creeping stems of grasses may be sympodial or monopodial in habit. Sympodial stolons sometimes form a flat pseudo tuft as in Yorkshire fog.

Rough-stalked meadow-grass is of interest here. The young seedling plant branches intra-vaginally and forms a tuft. Later tillers, however, develop extra-vaginally to form stolons. The offsets produced by the stolons are tufted, and in turn produce stolons. Rough-stalked meadow-grass is peculiar in that it shows both tufted and creeping habit.

The "Bulbous" Grasses

Not only are stolons and rhizomes found in different grasses, but corms and bulbs may occur. In timothy grass the first few internodes immediately above the soil level swell out to accommodate food stores and a pseudo-corm is produced. This is covered by brown or chocolate-coloured shrivelled bases of the lower leaf sheaths.

In tall oatgrass a number of internodes below soil level become swollen, the nodes not being particularly affected. The corms in this case resemble a string of small onions or very large beads. These resemblances confer on the plant its popular name of

" onion couch," " pearl grass " or " pearl couch." Each " bead " is a swollen internode, and the whole string breaks up easily into units. Each unit consists of one swollen internode and the node immediately below. It is thus complete with a bud accompanied by a supply of food. All these propagative devices for spreading the plant also confer perenniality.

Ptyxis, or the Arrangement of the Leaves in the Bud

The next character of importance in recognition is how the young leaves are arranged in the bud. The stem of all grasses is cylindrical (round in T.S.). When the young leaves in the bud are *rolled* round the stem the external appearance is cylindrical, and in T.S. the bud appears circular in outline. The leaf blades emerging from such a bud are curved about their long axis or mid-rib.

The leaves may be, not rolled, but folded over the stem. In these cases the fold runs up the long axis of the blade at the

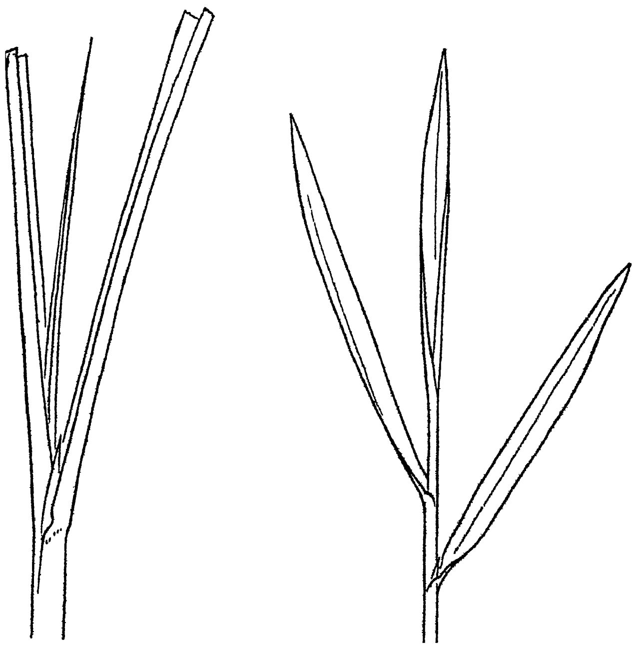


FIG. 47
Left Leaves emerging from " folded in the bud "
Right Leaves emerging from " rolled in the bud "

main vein or mid-rib. The external appearance of a bud of this character is of a two-sided, flattish structure, elliptical in T.S. The leaf blade newly emerged from a bud of this type is seen to expand like an opening book.

The two conditions, rolled and folded, may be readily recognized in the field by taking a grass bud lightly between the forefinger and thumb and rolling it about. The " rolled-in-the-bud " grass rolls easily. The " folded-in-the-bud " seems to " bump," and the finger is pressed away from the thumb and then allowed to come nearer. This provides a very useful feature in identification. For example, Italian ryegrass and perennial ryegrass are very closely related and very similar in appearance when not in flower, yet Italian ryegrass is readily seen to be " rolled in the bud," while perennial ryegrass is " folded in the bud."

The Leaf Sheath or Petiole

Taking the several parts of the leaf in turn, the sheath may be dealt with first.

On the sheath a keel may be present or absent. The keel when present runs up the back or spine of the sheath and is formed by the accentuation of the main vein. In some grasses other veins are also of interest. In wood melic grass the main vein and two intermediate lateral veins are protuberant and the sheath appears four-sided or square in transverse section. Again, in many water grasses the veins are well developed with many cross connections forming a network, and the sheath appears " netted." In some grasses the margins of the sheath are grown together and give it the character of an entire or tubular structure as opposed to those in which the leaf sheath is not united, described as split. Often this character is not easily determined with certainty because growth of the bud may cause splitting of an entire sheath.

The Grasses with Coloured Leaf Sheaths

In Yorkshire fog the veins are stained with red dye and appear as fine pink lines running vertically up the sheath. In many other grasses the leaf sheaths are coloured uniformly, at least at their bases. The leaf sheath is a beautiful purple red in the ryegrasses and in meadow fescue, an orange-yellow in dogstail, or violet-cum-chocolate in meadow foxtail.

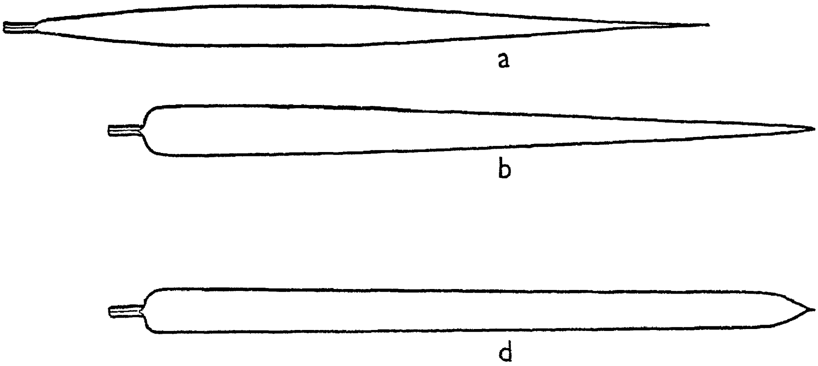


Fig. 48

Grass leaf-blade outlines

(*a*) Narrowing towards base and apex, broadest part $\frac{1}{3}$ up from base—false brome

(*b*) Broadest at base, narrowing all the way up, apex pointed—cocksfoot

(*c*) Margins nearly parallel, apex blunt—ryegrass

(*d*) Margins parallel, apex shouldered—smooth-stalked meadow-grass

The Hairy Grasses

The presence or absence of hair, not only on the leaf sheath but on all other parts, should always be noted. The amount of hair on a hairy grass tends to vary with climatic conditions, being more pronounced in dry and less well developed in wet situations.

The Blade or Lamina of the Leaf

The leaf blade provides many characters useful in recognition. Grasses may be formed into two classes, depending on whether the blade is fully expanded and flat or forms a long, thin, hair-like bristle.

It should be realized that the flat expanded lamina presents for inspection a definite outline, two surfaces (upper and lower), two ends (base and apex), two margins, and that the green colour is not usually uniform over its whole area. All these may provide good clues to the identity of a given grass.

Outline of Blade

The outline of an expanded grass blade usually resembles that of some form of a spear-head with curved sides. The two sides,

however, may be straight and parallel, giving a strap-shaped outline. In those cases where the sides are not straight the blade is not of the same breadth over its entire length, and the point of greatest width should be noted.

The Apex and Base of Blade

The apex of the leaf-blade may gradually taper to a point, or the sides may be parallel almost up to the apex and then form "shoulders." Similarly, in some species, the base of the blade continues quite broad and "comes in" quickly, while in others it narrows gradually from a point of greatest breadth down to the breadth of the stem diameter.

The Surfaces of the Blade

In some kinds of grass the surfaces of the leaf blade are dull, and in others shiny. For example, the leaf blades of perennial or Italian ryegrass are shiny on their lower surfaces but quite dull on the upper. When a field of leafy ryegrass is disturbed by a light breeze, waves of light appear to ripple over it, due to the wind altering the posture of the leaves or altering the angle the leaf makes with the light source. In one part of the field the shiny undersides are turned upwards and reflect light, while in other parts the dull upper surfaces have returned to their normal position. The striped appearance often seen in a grass-field after rolling is due to the same sort of cause. The roller passing in one direction bends the blades so as to reflect light in one particular direction, and in travelling in the opposite direction the blades are bent so as to reflect light in a direction different from the first.

Ridges and Furrows on the Surface

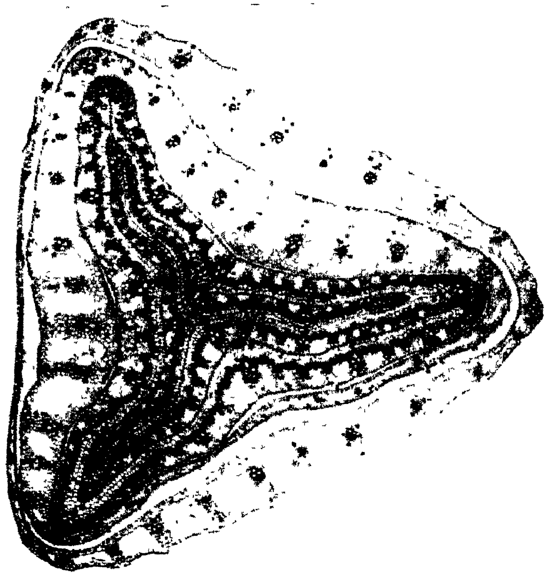
Another character to be examined in the blade is the presence or absence of ridges and furrows. The ridges occur in lines, where the veins with their accompanying sclerenchyma form a thickness; the furrows are the spaces between occupied only with mesophyll. Green colour does not occur in conducting tissue nor in the sclerenchyma; hence, if the blade is viewed by transmitted light, the ribs and furrows appear as alternate dark and light lines. Ridges and furrows are confined to the upper surface, and are not commonly found on the under surface. The mid-rib in

PLATE 33 SOME "BULBOUS" GRASSES

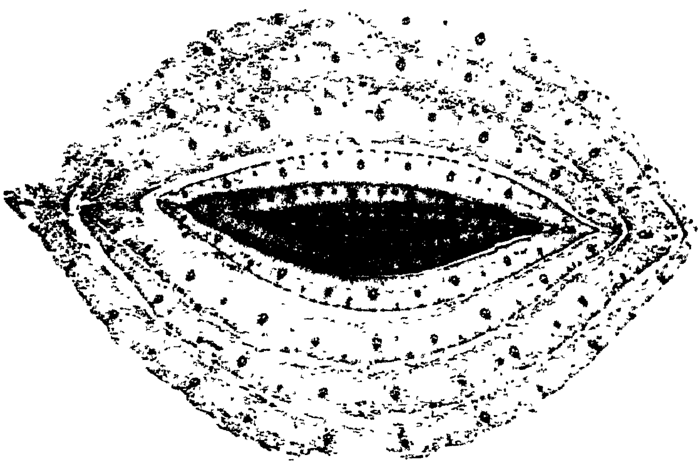
Tall Oat Grass

Timothy (Herd's Grass)

Purple Molinia. (Note the cord roots)



T.S. Bud of a Sedge. Phyllotaxis $\frac{1}{3}$



T.S. Bud of Cocksfoot. Like all grasses, phyllotaxis $\frac{1}{2}$. The leaves are folded in the bud

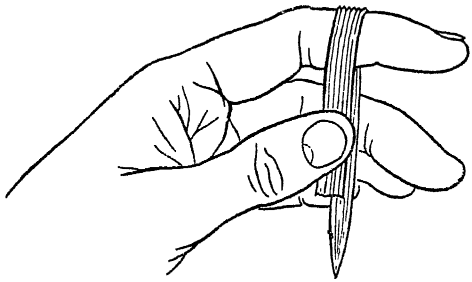


FIG. 49
How to view leaf-blade ridges in the hand specimen

many grasses is well developed on the under surface, and suggests a keel as seen in a boat. A grass blade with a protuberant mid-rib on the under surface is said to be keeled.

The shape of the ridges is best seen by looking at a transverse section. In the field this character may be determined by bending the intact leaf over the forefinger of the left hand and holding the hand up to the light. Using a hand lens the leaf surface is then viewed in contour as it "goes over the horizon." The tops of the ridges may be flat, giving an appearance like castellated ramparts, or they may be rounded at the apices or each come up to a sharp angular ridge.

Motor Tissues or Hinge Cells

In some grasses there are in the upper epidermis lines of large cells with thin uncuticularized walls. These lines of thin-walled tissue run parallel with the long axis of the blade, very often alongside the mid-rib or alongside the mid- and intermediate ribs. In dry weather these cells lose water easily and shrink. This causes the leaf to roll up to form a tube with the upper surface inside. As will be explained later, this protects the leaf from being dried out. Thin-walled tissues of this type are known as motor-tissues or hinge-cells.

Roughness of Surface

Another point about surfaces arises from the fact that the blades of many grasses develop surface emergences, hairs strengthened or coated with silica. These hairs are often curved like shark's teeth or cat's claws, with the points directed either towards the

FIG. 50

Emergences on surface of leaf blade. L. S. toothed blade of tufted hair grass. These "teeth" give the diagnostic character of downwards or upwards rough, depending on their direction of curvature

base or the apex of the lamina. By passing a finger-tip or the tongue along the leaf surface from base to apex or from apex to base, the direction in which these emergences point may be ascertained. If the finger passes against the points the surface registers as rough, but if it passes over the curved backs of the hairs a smooth surface is suggested. If the roughness is apparent when the finger is pulled downwards from the apex to the base of the leaf, the condition is described as downwards rough. If the roughness is felt in the reverse direction, the blade is said to be upwards rough.

The Ligule

Considering now, not the blade, but the ligule the comparative length should be noted. It may be very long and pointed as in tufted hair grass, or so small as to be a mere ridge as in many of the fescues. In three grasses (purple molinia, decumbent heath grass and common reed grass) it is reduced to a fringe of hairs.

The Auricles

As regards the auricles, chief interest turns on their presence or absence. If present their length is important, and whether they are curved so as to clasp the stem or not.

Grasses with Bristle Blades

Turning now to the bristle-bladed grasses, there is very little detail to be seen in the hand specimen of the blade though the transverse section may be highly diagnostic. That of wavy hair grass or moor mat-grass is solid with a median furrow. In sea meadow-grass it is a U-shaped channel. In the bristle-bladed fescues the form of the blade is due to the rolling up of the deeply-furrowed lamina which is caused by the action of lines of motor tissue. In the field the mode of formation of the bristle is not a good diagnostic point, and these grasses are usually differentiated one from the other by other characters.

For example, moor mat-grass is a perennial of tufted habit. The leaf sheaths persist for many years. The bristle blades are erect when young, later they assume a horizontal position, and after quite a short life they are shed. An old plant of moor mat-grass forms a compact tuft with persistent sheaths at the periphery, then a narrow band of complete leaves with their blades held horizontal and, in the centre, young entire leaves, the blades of which are held vertically.

In learning to identify plants by this or any other method it is advisable to see as many types as possible, arranging and re-arranging the members as they fall into different groups. For example, if one groups grasses according as the blades are rolled or folded in the bud, Italian ryegrass, being rolled, is separated from perennial ryegrass, which is folded, but both are brought together when rearranged in the " coloured leaf sheath " group.

Only by examining and re-examining, grouping and re-grouping, the grasses does familiarity and ready identification come. A composite table of the common British grasses is offered here (Tables II, III, pp. 128-132). In this they are so arranged that grasses possessing some prominent feature in common are associated. The student should regroup the various grasses in the table according to some other feature, and so see different relationships.

The Clovers and their Allies

The clovers and plants closely related to them are known as legumes. This name comes from the nature of their fruit, which is always a variation of a simple pod as seen in the pea or bean.

Those legumes which occur in grassland fields (excluding whins or gorse) are herbs. Some are annuals, others biennials

or perennials. The length of life in many cases depends on the variety of the kind in question and the climatic conditions under which it is grown. A number are perennial because of their creeping habit, or because of their ability to form stools.

The simplest way to deal with this somewhat mixed assemblage of pasture and hay type plants is to consider them group by group. As vegetative characters only will be considered here, the group with the simplest leaf will be treated first. Later, groups in an ascending order, determined according to the complexity of their foliage, will receive attention.

Whin or gorse is a woody shrub, with plain strap-shaped leaves. The tips of the branches form sharp points, rendering

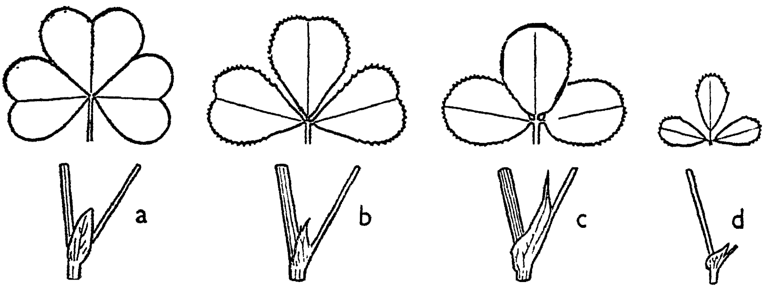


FIG. 51

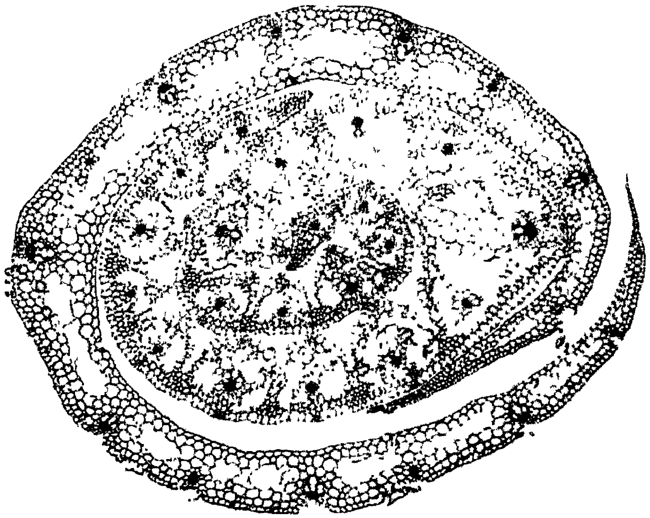
Leaves of some characteristic clovers (blades and stipules)

(*a*) subterranean (*b*) white
(*c*) strawberry (*d*) suckling

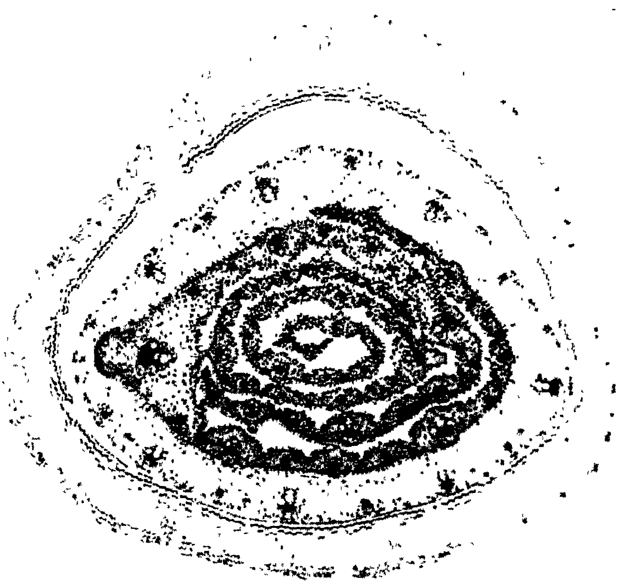
the plant extremely repellent to stock. It is sometimes cut-over, so that young stems may sucker from the stumps. These are not so hard and prickly as the adult shoot, and may be grazed by animals. In some districts the young suckers are cut, collected, crushed to a fibrous pulp, and fed to stock. Typically a shrub, the simple strap-shaped leaves and the branches which terminate in sharp points or spines render it easy to identify, and no-one could confuse this plant with the others listed here. Usually the plant is a nuisance and should be eradicated.

The True Clovers

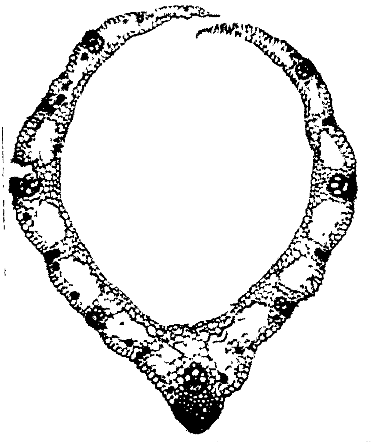
Of the more typical grazing and forage legumes, the first group is the true clovers. These always produce compound leaves formed of three leaflets. From this characteristic they derive their botanical name of *Trifolium*. In common usage, this name



T.S. bud Italian Ryegrass : rolled

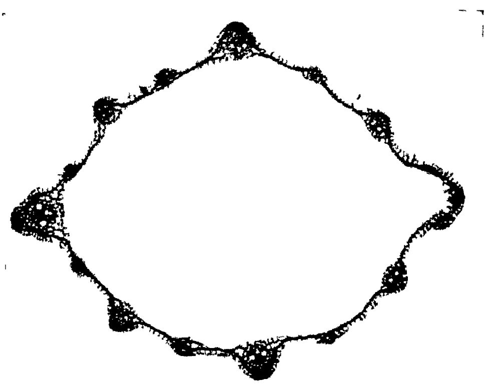


T.S. bud Schrader's Brome. Leaves rolled, but the presence of a prominent keel may suggest the folded condition in a hand specimen



Keeled, split sheath of Timothy Grass

Not keeled, split sheath of Tall Oatgrass



The four-angled entire sheath of Wood Melic Grass. The mid-rib (*on left*) forms one angle, the joined margins another, and two intermediate veins the other two

TABLES II, III

TABLE 11.—SUMMARY OF THE VEGETATIVE CHARACTERS OF THOSE LEAF-BLADES

	Name of grass	Habitat	Duration	Height	Habit	Hair	Arrangement in bud
1	Crested Hair Grass	limestone; dry soil near sea	P	B	tuft	hairy	F/R
2	Heath Grass	heaths and barren land	P	B	tuft; semi-prostrate	hairy	F
3	Downy Oat-Grass	Dry pasture on chalk	P	B	tuft	hairy	F
4	Perennial Oat-Grass	widely distributed; not common	P	T/B	tuft	usually glabrous	F
5	Perennial Ryegrass	good land	short P	B	tuft	glabrous	F
6	Dogstail	variety of soils; dry downs, etc.	short P	B	tuft	glabrous	F/R
7	Cocksfoot (Orchard Grass)	all medium and good soils	P	T	tuft	glabrous	F
8	Smooth-stalked Meadow-Grass	variable; stands heat, cold, and drought	P	B/T	rhizomes	glabrous	F
9	Rough-stalked Meadow-Grass	moist ground; water not stagnant	P	B	stolons and tufts	glabrous	F
10	Wood Meadow-Grass	shady places	P	B	tuft	glabrous	F
11	Annual Meadow-Grass	everywhere	A	B	tuft	glabrous	F
12	Canada Blue Grass	dry situations	P	B	rhizomes	glabrous	F
13	Floating Sweet Grass	ditches and shallow fresh water	P	B ?	stolon/rhizomes	glabrous	F
14	Reed Sweet Grass	shallow fresh water	P	T	stolons/rhizomes	glabrous	F
15	Yorkshire Fog	all soils, moist preferred	P	B/T	stools or short stolons	dense hair	R
16	Creeping Soft Grass	shade	P	B/T	stolons/rhizomes	hairy	R

GRASSES COMMON IN TEMPERATE REGIONS WHICH HAVE ALL THE EXPANDED

Sheath: Colour, etc.	Sheath: Split	Auricles	Ligule	Notes	
hairy	split	none	absent or much reduced	ribs of blade prominent; motor tissue at mid-rib	1
hairy	split	none	a tuft of hair	the only grass with leaves folded and ligule a tuft of hair; roots stringy	2
hair in rows	split	none	long and pointed	median lines on either side of mid-rib	3
—	split	none	basal short; culm long	blade has outline like smooth-stalked meadow-grass; blades tend to fold up	4
red	doubtful	small, clasping	short	blades dark green; upper surface dull, lower shining	5
yellow	split	none	short	blades dull on upper surface; shining on lower	6
—	entire; keeled	none	prominent	large, broad-bladed tuft. Shows much burn	7
—	entire	none	short and blunt	blades with parallel edges; apex shouldered to form blunt tip	8
—	entire; keeled	none	short; top of culm long	blade edges not parallel; apex not shouldered	9
—	split	none	short or absent	the bud suggests rolled; blade long, narrow, ribless; a variable grass	10
—	?	none	distinct; keeled	blades often "puckered"; apex blunt	11
—	?	none	short, blunt	folding in bud extreme; shoot flattened	12
striated	entire	none	distinct	two triangular patches where sheath meets blade; sheath of spongy texture	13
netted	entire	none	short	triangular patches and spongy texture of sheath as above	14
red lines	split	none	distinct	foliage sap green and grey; softly hairy to touch	15
red lines	split	none	distinct	extra vaginal tillers; definite stolons or rhizomes NOT stooling	16

	Name of grass	Habitat	Duration	Height	Habit	Hair	Arrangement in bud
17	Heath False Brome	heaths	P	B	slight stolon	hairy	R
18	Wood False Brome	shade	P	B	tuft	hairy	R
19	Purple Molinia	wet moor	P	B	tuft	hairy	R
20	Golden Oat-Grass	dry	P	T	tuft	hairy	R
21	Wall Barley-Grass	dry roadsides	A	B	tuft	hairy	R
22	Meadow Barley-Grass	stiff clays, etc.	P	B	tuft	hair on lower sheaths	R
23	Couch-Grass	almost everywhere	P	T	rhizomes	hairy	R
24	Bearded Wheat-Grass	widely distributed in shade; not common	P	T	tuft	hairy	R
25	Sweet Vernal Grass	wide range; best on good soil	P	B	tuft	hairy	R
26	Soft Brome	ubiquitous weed	A	B	tuft	hairy	R
27	Wood Brome	shade	B/P	B	tuft	hairy	R
28	Field Brome	poor soils	A/B	B	tuft	hairy	R
29	Sterile Brome	waste land and woods	A/B	B	tuft	hairy	R
30	Bent Grass	poor pasture	P	B/T	stolons/ rhizomes	glabrous	R
31	Meadow Foxtail	moist meadows	P	T	loose tuft; stools	glabrous	R
32	Slender Foxtail	stiff soils	P	B	stolons	glabrous	R
33	Floating Foxtail	semi-aquatic	P	B	diffuse tuft	glabrous	R

Continued

Sheath: Colour, etc.	Sheath: Split	Auricles	Ligule	Notes	
hairy	split	none	fringed with hair	blades erect and tend to roll up; plant forms circular patches	17
hairy	split	none	prominent; blunt	blades drooping; pale sap green; tapering to base and apex	18
smooth; no keel	split	none	absent, or a tuft of hair	lowest internode swollen; blade tapers to base and apex; cord roots	19
silky hairs	split	none	blunt	blades thin, dry, pale green; silky hair both surfaces	20
—	split	large and overlapping	short and blunt	blade thin; both surfaces hairy	21
lowers hairy	split	small	short	blades hairy on upper surface; glabrous and glossy on lower	22
no keel; hairy	split	small, pointed	short and pointed	hairyness variable; usually most on upper surface of blade and lower sheaths	23
—	split	small, pointed	short, blunt		24
sparse hair	split	blade forms ledges	blunt and thin	a sweet-scented grass; blades short, light green, with low, flat ribs on upper surface	25
—	entire	none	short, ragged	The brome grasses are widely distributed; there are many kinds, none easily recognized in vegetative condition; these here are examples	26
—	entire	none	short, ragged		27
—	entire	none	short, ragged		28
—	split	none	short, blunt		29
—	split/entire	none	variable	a group of many variable forms; blades always ribbed	30
purple, turning chocolate	split	none	blunt; variable length	foliage dark green; blade broadest near base; ribs low, flat topped	31
rough	split	none	—	ribs acute, not flat topped	32
—	split	none	long	tillers kneed at practically every node	33

TABLE III.—GRASSES COMMON IN MORE TEMPERATE REGIONS WHICH HAVE THE MAJORITY OF THE LEAF BLADES IN THE FORM OF A BRISTLE

Name	Habitat	Duration	Habit	Sheath	Ligule	Auricle	Notes
Sheep's Fescue	poor, dry soil	P	compact tuft ; all tillers intra-vaginal	split ; tend to persist	very small or absent	hump-like cartilaginous	These form a group of intergrading forms, probably interfertile and producing intermediates
Various leaved Fescue	poorer soils	P	compact tuft ; some tillers extra-vaginal	entire	very small or absent	ditto	All form the bristle by a more or less permanent fold developed in bud and maintained in development
Chewing's Fescue	poorer soils	P	tuft ; extra vag. tillers ascend	entire	very small or absent	ditto	In all, the roots are fibrous
Red Fescue	poorer soils	P	stolons/rhizomes ; no tillers intra	entire, pink	very small or absent	ditto	various leaved has radical leaves, bristles and cauline leaves expanded
Rat's-tail Fescue	road sides ; waste land	A	tuft	entire	much reduced	much reduced	a fibrous rooted weed ; showing a number of forms
Moor Mat-Grass	moors and hill pasture	P	compact tuft	split ; persists	short, blunt and thick	none	nearly solid and permanent bristle ; young blades erect, older horizontal ; roots cord-like
Wavy Hair Grass	dry hills	P	tuft	split	long and thin	none	roots fibrous ; blade nearly solid and permanent bristle
Silvery Hair Grass	poor hill	A	tuft	entire	small	none	needle-like bristle
Sea Meadow-Grass	sea sands	P	rhizomes		short	none	permanent rolled blade forms bristle

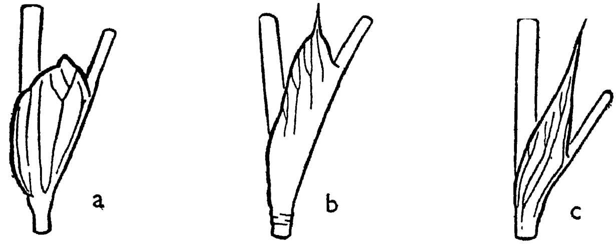


FIG. 52—Stipules

(*a*) crimson clover (*b*) red clover (*c*) alsike clover

The plants are of somewhat similar habit; their stipules provide a simple means of identification

is sometimes applied to one particular member, which is also, and more conveniently, called crimson clover.

The individual leaflets of clovers may be practically sessile on the top of the leaf-stalk or petiole or each may be carried on a short leaflet stalk. The leaflet stalks may be not all of the same length. The base of the petiole where it joins the stem is expanded into little wing-like side-pieces. These paired structures, one borne on either side of the petiole, are called *stipules*. The stipules differ in size or shape in different legumes, and provide features for identification.

Tillering in Clovers

The biennials by production of short branches from a very short main axis may form rosette plants in the first year. In the second summer, as flowering approaches, these branches lengthen and the plants are said to shoot. Just as in the grasses, the term tiller may be applied to the shoots and tillering to the process.

Some legumes form stolons, and at least one produces rhizomes.

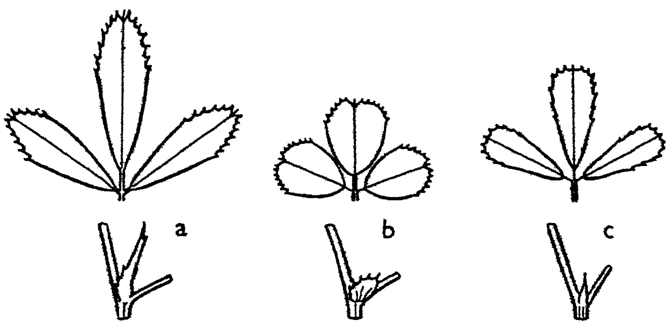


FIG. 53

Leaves and stipules of (*a*) lucerne (*b*) black medick (*c*) sweet clover

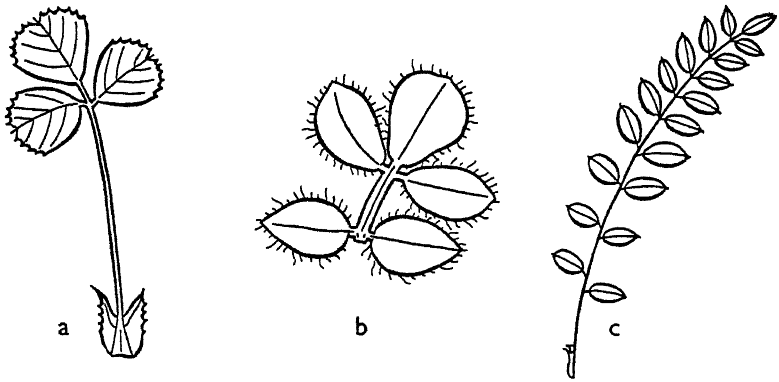


FIG. 54

Complete leaves of (*a*) black medick, (*b*) bird's-foot trefoil, (*c*) bird's-foot (seradella)

Features of the Leaflet

The shape or outline, the margin, base, and apex, etc., of the individual leaflets often provide features for identification. One very useful character is the tip of the leaflet. In clovers this may be pointed, rounded off, or indented, but a short pointed structure never arises in the base of an indent. This mucronate point is never seen in the clovers, but is invariably present on the leaflets of their two trifoliate relatives, the medicks and sweet clovers (melilots).

Legumes often Confused

The medicks include yellow trefoil or black medick, a semi-prostrate annual, and lucerne or alfalfa, a perennial which forms a stool. The sweet clovers are also trifoliate, and like the medick have a mucronate point. The annual forms of melilot are unlike the annual medicks vegetatively in that they grow erect. The longer-lived melilots are not to be confused with lucerne, for they do not form stools.

Trefoil, Bird's-foot Trefoil, and Bird's-foot

Plants sometimes confused with black medick because of a similarity in naming are the bird's-foot trefoils. This confusion is worse confounded by the fact that still another and quite different plant, seradella, is sometimes called bird's-foot. The three plants are clearly differentiated vegetatively. Yellow trefoil or black

medick or non-such, as it is variously named, has trifoliate leaves. Bird's-foot trefoil has five leaflets per leaf. Bird's-foot has more than five leaflets, usually some seventeen or nineteen. They are arranged in pairs up the mid-rib with an odd one terminal in the same manner as the barbs of a feather, and the leaf as a whole is said to be pinnate. The vegetative features used to differentiate these three plants may be summarized in tabular form :

yellow trefoil—leaf trifoliate
bird's-foot trefoil—leaves pinnate of five leaflets
bird's-foot—leaf pinnate, of many more than five leaflets

Bird's-foot Trefoil

Returning to consideration of bird's-foot trefoil, the leaf has two pairs of leaflets plus a terminal one. The two lowest leaflets are situated close to the stem, while the remaining three are distal, and a comparatively long extent of bare mid-rib intervenes between the basal pair and the distal trio. The basal pair might be mistaken for stipules, but they are of characteristic leaf structure. The true stipules in this plant are minute and difficult to see.

There are a number of bird's-foot trefoils, only two of which are commonly sown. Marsh or greater bird's-foot trefoil is found usually where moisture is plentiful, and is a bigger plant with stems longer and more trailing. The other occurs on drier, poorer land, and the stems are shorter and more erect.

Kidney Vetch

Kidney vetch, another legume sometimes sown, often shows two types of leaf. The leaves produced in the early part of the plant's life are simple, but the fully adult leaves are compound of three to four pairs of leaflets plus a terminal one. The terminal is often larger than the paired members. In the adult ground-leaves the leaflet pairs are close together on the mid-rib, while those of the cauline leaves are spread quite widely apart.

Sainfoin

Sainfoin, which is often grown as a forage plant, has compound pinnate leaves. Two varieties are grown : a short-lived type known as French or giant and a perennial known as old common.

The leaves in both varieties are stalked and have five to seven pairs of leaflets plus the terminal. No vegetative character separates the two.

Seradella

Seradella is a slender spreading annual sometimes used as a green manure on sandy, dry soils. The one grown is hairy and the stems are spreading or trailing. There are five to ten pairs of leaflets plus a terminal in each pinnate leaf.

Lupins

Lupins have compound leaves but the leaflets are not arranged in pairs on a mid-rib as in the previous examples. All the leaflets are in a group at the top of the leaf stalk. Because of the leaf's likeness to the fingers of an open hand the leaf is said to be digitate.

When flowers and fruits are present it is possible to discriminate easily between these legumes, but it is also possible to do so with some degree of accuracy by purely vegetative means. Table IV (pp. 138–141) provides in summary form details of the more significant characters.

Anatomical detail in identification

All the methods outlined so far have dealt with morphological features but details of anatomy can also be used for identification. The disposition of tissues and the elements which go to form them all show small differences which are constant as between one kind of plant and another.

This kind of work is highly specialized, and no more than an outline may be presented here. For example, if small pieces of grass leaf are submitted for identification, the bristle-bladed grasses as a group are soon recognized. If a transverse section is made, then the differences in type of bristle at once give a clue to the identity of the specimen.

With grasses whose blades are expanded, it is advisable to select a typical fragment and at once make a transverse section. When this is examined, the presence of ridges and furrows, hairs on the surfaces, the disposition of sclerenchyma, all give clues to the identity of the specimen. In many grass leaves the strengthening tissue is in shape like a girder, and in transverse section is seen as I with perhaps a vein cut across in the waist.

TABLE IV

TABLE IV.—SUMMARY OF FEATURES USEFUL IN THE

(A = Annual ; B =

PLANT		LEAF
NAME	LIFE SPAN AND HABIT	
		ALL ADULT LEAVES OF THREE
Crimson Clover or " Trifolium "	A. Neither stool-forming nor creeping	stipules broad and blunt; ground leaves long petiole; cauline leaves short petiole
Red Clover	A or short P. Rosette in winter, erect tillers in summer	stipules broad with sharp point; petiole short, especially on cauline leaves
Zigzag Clover, Cow-grass (see Notes)	P. Creeps by rhizomes	stipule narrower than red; petioles like red
Berseem, or Egyptian Clover	A. Neither stool-forming nor creeping	stipules long and pointed; petioles like red
Alsyke, Alsike, or Swedish Clover	P. Rosette in winter, tillers erect in summer	stipules long, narrow, with prolonged pointed apex; petiole long
White Clover	P. Main axis short; many stoloniferous branches, which root freely	stipules small, sharp-pointed; petioles from stolons long and erect
Strawberry Clover	P. Main axis short; axillary stolons rooting sparsely	stipules long, pointed, encircling stolon; petioles long and erect
Subterranean Clover, " Sub " Clover	A. Stems long, trailing, prostrate, hairy	stipules long-pointed, stand away from stem; petioles long, erect, hairy
Suckling Clover	A. In short sward stems prostrate, erect in long herbage	stipules small, sharply pointed, margins entire; petioles short
Black Medick, Nonsuch Yellow Trefoil	A/B Ditto	stipules large, broad, sharply pointed, toothed margins; petioles long at ground, short on cauline leaves

Biennial ; P = Perennial)

LEAFLETS	FLOWER HEAD AND PETAL COLOUR	NOTES
LEAFLETS—TRIFOLIATE		
sessile, broadly heart-shaped ; margins entire, fringed hair ; hair on surfaces	cone-shaped spike ; terminal on tiller	a hay type plant, white flowered varieties known
oval or elliptical on short stalks, all equal ; margins entire ; glabrous/hairy with white crescentic mark on each	globular on short stalk ; pink, red, purple	variable as to habit ; never creeping ; classed according to flowering into wilds, earlies, lates
narrowly elliptical, pointed apices ; otherwise same as red clover	same as red clover ; pink	" cowgrass " of seed trade is a red clover , this plant is a wild weed
narrowly elliptical, entire margins, glabrous, sessile	egg-shaped ; cream	there are three varieties
regularly elliptical, glabrous, with no crescentic mark ; each sessile with toothed margin	flat ; white or cream, tinged pink	the whole plant is devoid of hair
heart-shaped with notched apices ; sessile or stalks very short ; margin toothed, hairless ; crescentic white mark on each	flat, on a stalk longer than petiole ; white or cream	3 main forms available—wild, Dutch or commercial, and giant (*e.g.* Ladino)
broadly elliptical on short stalks ; glabrous with toothed margins ; faint crescentic mark	globular on long stalk ; pink	resembles white, but stipules and flower head differ, less roots on stolons
broadly heart-shaped, sessile, hairy ; margins entire	3 to 4 flowers terminal on axillary branch ; yellow, brown-purple veins	flower heads held up to light, later bend down to place fruits in soil
longer than broad, broadest near apices ; stalk of terminal longest ; margins toothed shoulder to apices ; few hairs on lower surface	nearly globular on short stalks ; yellow	this includes a number of forms distinguished from medick by absence of mucronate points, etc.
almost identical with suckling but mucronate point at apices	same as suckling clover	very like suckling ; differs in leaflet, stipules, and fruit

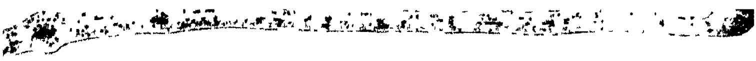
PLANT		LEAF
NAME	LIFE SPAN AND HABIT	
Lucerne or Alfalfa	P. Stooling ; stems erect ; stout tap-root	stipules broad at base, sharp-pointed apex, toothed margin; petioles short
Sweet Clover, Melilot, Bokhara Clover, etc.	A/B. Small crown erect ; stems tall	stipules small, narrow ; margin entire ; petioles short
		ALL ADULT LEAVES OF MORE
Bird's-foot Trefoil	P. Prostrate in open, erect when crowded	stipules very small ; leaves sessile
Kidney Vetch	P. Rosette in winter ; erect tillers in summer	stipules small and pointed ; petioles very short
Seradella or Bird's-foot	A. Weak trailing stems from small crown	stipules very small ; petioles very short
Sainfoin	B/P. Forms broad crown ; stems erect, 1–2 feet	stipules broad at base, tapering to a point ; petiole long and hairy
Vetches or Tares	A. No crown ; many straggling stems from much-branched primary	stipules small, pointed, with dark purple blotch
Field Bean, Horse Bean, Tick Bean	A. Few, erect, hollow stems, winged at angles	stipules small, wing-like, toothed ; petiole short ; midrib channeled
Field Pea, Partridge Pea, Maple Pea	A. One or few straggling hollow stems, waxy bloom	stipules large, spreading coloured purple where they meet stem
Annual Lupin	A. Few not quite erect stems from crown on stout tap-root	stipules small, broadest at base, pointed ; petioles long, stout

continued

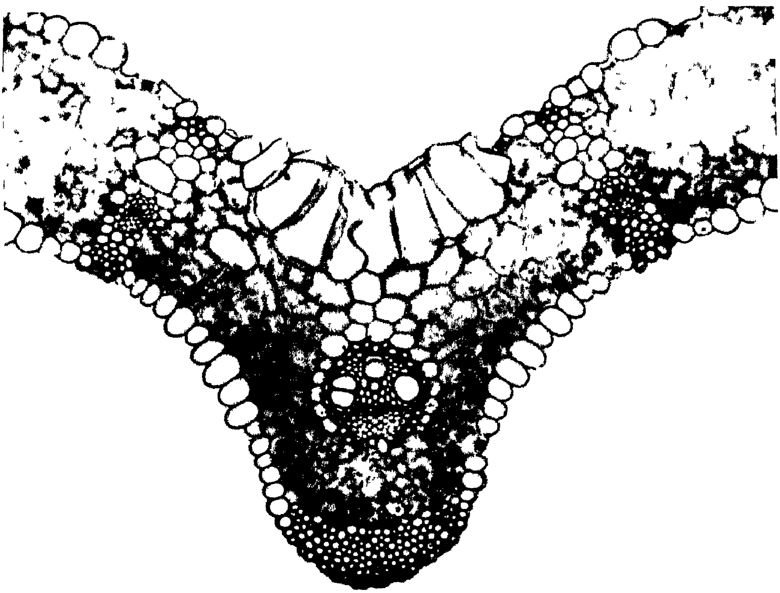
LEAFLETS	FLOWER HEAD AND PETAL COLOUR	NOTES
larger than yellow trefoil, otherwise very similar	simple raceme; blue	a related form with yellow flowers; intercrosses to give valuable though sterile hybrids
elliptical; teeth all round margin, otherwise similar to above	erect raceme; white, cream or yellow	as a rule yellow-flowered forms are annuals, white-flowered biennial; sweet smell due to coumarin

THAN THREE LEAFLETS

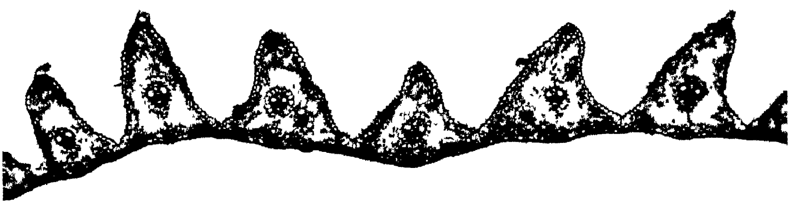
5; upper 3 broad near apices, narrow at base; lower 2 broadest near base; stalks short; margins entire; short hairs	5; flowers on short stalk; yellow	simulates a trifoliate leaf with pair large stipules; flower buds crimson prior to opening
variable; always longer than broad on short stalks; each entire with soft hair	flat heads in pairs, each on short stalk	a single plant shows variety of leaves from simple entire to 4 pairs leaflets plus terminal
5–10 pairs and terminal; each small, oval, often hairy on short stalk	2-3 flowers on short axillary branch; white or pink	useful as a green manure on dry sandy soil
5–7 pairs plus terminal; each narrowly elliptical on short stalk; margin entire	raceme; pink, red to purple	two varieties cultivated—common or English, and Giant or French
6–7 pairs (terminal forms tendrils); each elliptical with mucronate point	single flowers or pairs on short stalks; red-purple	" winter " vetches are hardier than " spring " variety
1–4 pairs plus small tendril-like terminal; elliptical, hairless; margins entire	2–6 flowers on axillary, racemes white with black patch on wing petal	winter beans, hardy and slower growing; spring beans not hardy, quick growing; no other difference
2–3 pairs (elliptical) proximal and 2–3 pairs as tendrils distal from stem, plus tendril terminal	1–2 flowers terminal on short axillary branch, purple; wing petals darker	procumbent, unless supported; often grown with oats for soiling and silage
5 long narrow arise in whorl at top of petiole; small in blue lupin, large in white, inter. in yellow	many-flowered, long raceme blue, white or yellow, depending on variety	feed with care, bitter alkaloid present; " sweet " non-poisonous varieties being bred



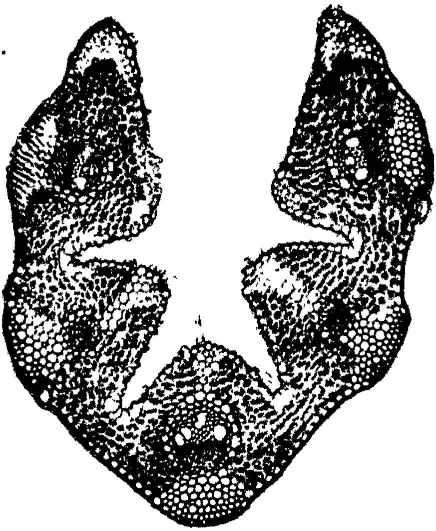
T.S. The left half of an expanded blade



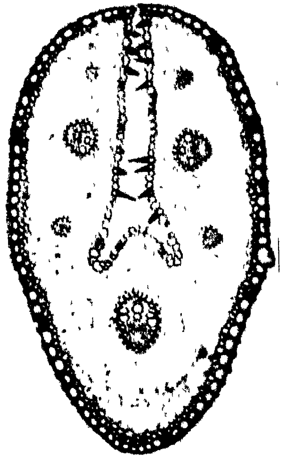
T.S. Centre of blade of Cocksfoot
Note the motor-tissue on upper surface above the mid-rib ; the large mass of sclerenchyma below



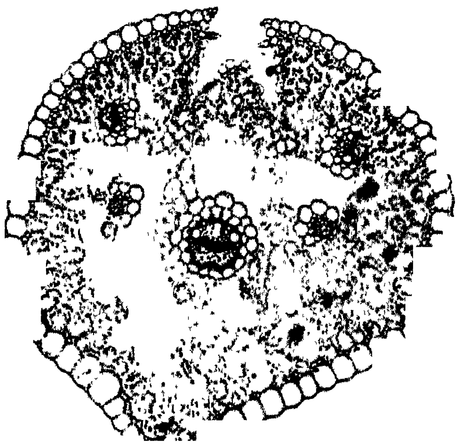
T.S. Leaf blade of Tufted Hair Grass to show ridges and furrows



Bristle blade of Moor-Mat Grass



Bristle blade of Sheep's Fescue



Bristle blade of Wavy Hair Grass

These three grasses show a progression in the evolution of the bristle blade. Note the motor-tissue in Moor-Mat; the bristle of wavy hair is permanent and cannot expand

BOOKS FOR FURTHER READING

ARMSTRONG, S. F. *British Grasses* (Cambridge University Press, 1937)

LEWTON-BRAIN, L. *On the Anatomy of the Leaves of British Grasses.* Trans. Linnean Society (Ser. 2 Botany) 2 (4), 1883

SOLEREDER, H. *Systematic Anatomy of the Dicotyledons* (2 vols.), English trans. (The Clarendon Press, Oxford, 1908)

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CHAPTER VII

THE FLOWER: ITS SEVERAL PARTS, THEIR NATURE AND ARRANGEMENT

ALL the parts of the plant so far studied here have been those involved in functions other than reproduction. During the life of any individual plant a period of time is spent in this asexual, vegetative condition. The organism, while in this condition, is said to remain in the vegetative phase. Sooner or later, depending on the nature of the plant and the conditions under which it lives, organs connected with reproduction are formed and the plant enters the reproductive phase.

The parts involved in reproduction should be regarded as further modifications of form for special function. The leaf is the organ chiefly affected. Leaves considerably changed in appearance and structure are grouped in special ways to constitute what is called a flower.

SEXUAL REPRODUCTION

Biologically the whole significance of the flower derives from its primary functions which are first to produce, and later to facilitate the meeting of two highly specialized cells, the sex-cells or *gametes*. The meeting and subsequent fusion of these two cells results in a completely new individual. The immediate result of sex-cell fusion is one cell, the *zygote*, which in its turn by somatic cell-division gives rise to all the cells of the body of the new individual. The sex-cells are a product of one generation; the result of their meeting and fusion is a new generation. The sex-cells are the connecting link or bridge between one generation and the next.

The Benefits derived from Sexual Reproduction

This process of transference of life from the old to the new generation is full of hazards and difficulties, but it is necessary, for not only does it lead to increase in numbers and perpetuation of the kind, but by it variations are produced which are subjected to selection. Progressive evolution thus becomes possible. In addition to these primary benefits, many of the ills that plant life is subject to are not transmitted through the sex-cells, and the effects of senility also are cast off by sexual reproduction. Re-

juvenescence and health are regained for the new generation. All these points should be borne in mind, as they provide a background of " reason " for the complications of the processes whereby the end is achieved.

The Inflorescence

Given that the conditions obtaining both inside the plant and in the environment induce flowering, it is found that the blossoms produced are located in a more or less specialized region called the *inflorescence*. The inflorescence takes many forms. Each flower may be solitary on a long stalk as in the tulip, or a number may be produced close together on an extended axis as in wheat, or crowded together on a flattened short axis as in the sunflower.

The axis of the inflorescence may be variously branched. In short, the inflorescence is a part of the shoot system bearing specially modified leaves which form in groups. Each group is a flower. The flowers in the inflorescence are arranged and grouped in characteristic ways.

The characteristics of the flowering region or inflorescence vary from one kind of plant to another. The differences are of peculiar interest to the academic botanist. Some of them indicate a rather primitive degree of development in the evolution of these features, others show a high degree of organization. All the evolutionary trends are towards improving the chances of the two sex-cells meeting, or increasing the protection of the offspring, or facilitating the dissemination of the seeds. Economy in the use of material, along with the attainment of a higher degree of efficiency, has governed the processes of evolution in the inflorescence.

The Flower

The individual flower, typically, has four well-defined kinds of parts. These are sepals, petals, stamens, and carpels. Each individual of each kind is formed from one modified leaf, and each kind has a peculiar function to perform. When the function performed by a part has been taken over by development elsewhere, then that part may be omitted from the flower. Again, any one of the parts may have developed a secondary function in place of, or along with, the primary function, and in virtue of this is modified still further as to structure. Examples of one or other of these standard parts being dropped out altogether will be offered later.

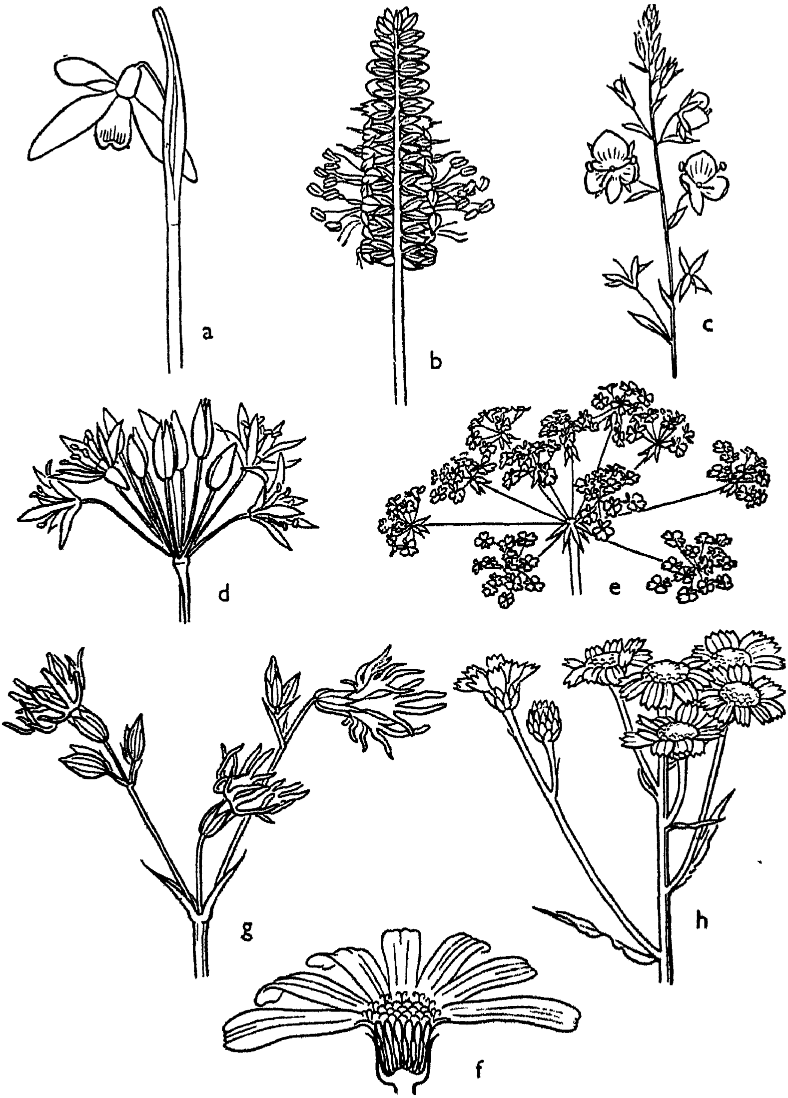
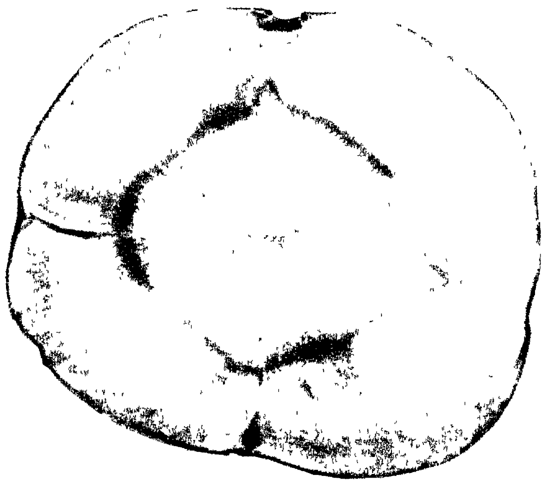


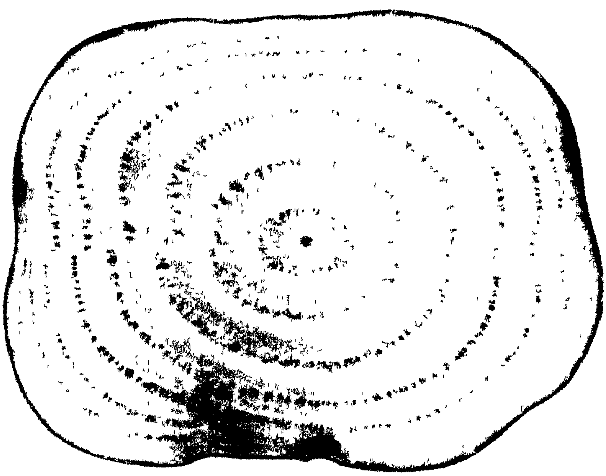
Fig. 55

Types of Inflorescence

(*a*) Flower solitary; (*b*) flowers sessile on unbranched axis, a spike; (*c*) flowers stalked on an unbranched axis, raceme; (*d*) flowers stalked on a contracted axis, a simple umbel; (*e*) flowers stalked on a series of contracted axes, a compound umbel; (*f*) flowers sessile on a contracted axis, a composite head or capitulum; (*g*) the axis terminates in a stalked flower and branches arise in the axil of two bracts, a cyme; (*h*) composite heads borne on branches



T.S. of carrot or parsnip (lignified tissue stained red)
In a good quality specimen the central core of xylem should be narrow and the cortex wide



T.S. of sugar beet, mangold or garden beet (lignified tissue stained red)

The product of five cambiums is clearly seen. The activity of the most recent (sixth) cambium is seen near the surface. The phloem appears white. The inter-ring parenchyma is also shown

COLOUR PLATE X SS IDENT CATION

Some grasses develop a characteristic coloration of the lower leaf sheaths. Four examples are seen here: (*a*) Meadow Foxtail (chocolate); (*b*) Ryegrass (red); (*c*) Yorkshire Fog (red veins); (*d*) Dogstail (yellow)

Flower Morphology: Reference Points and Lines

Just as in other studies of form, it is necessary in floral morphology to define first the " landmarks " or points and lines of reference to be used.

The flowers may be regular ; that is to say, all the individuals of each kind of part in the flower are the same size and shape. Or the flower may be irregular, when any kind of part, say the petals, will show members differing in size and in shape.

Irrespective of these differences there will be in the flower a " geographical " centre where the " seed-box " or ovary is placed. A series of concentric circles may be imagined as circumscribing this centre. The members of a kind of leaf, say sepals or petals, will be seen to lie on one of these circles. Floral parts are borne on a small axis called the *torus*. By reference to such imaginary circles the relative position close to, or away from, the centre may be defined for any individual part. When the number of leaves of a particular kind is large, they may be arranged on the torus in a tight ascending spiral. An example of this is seen in the stamens of a buttercup.

Another guide line is seen when the main axis of the inflorescence or its branch (when the axis is branched) is held up in such a way that an imaginary line passes from the observer's eye through the centre of the flower to the centre of the axis. This line bisecting the flower is called the anterior-posterior line. The posterior aspect of the flower is that next to the " post " or axis, while the anterior aspect is that towards the observer's eye. A line running through the centre of the flower at right angles to

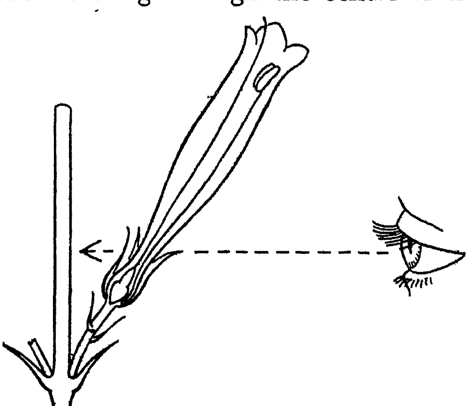


FIG. 56

The line from the eye to the axis in the drawing passes from the anterior to the posterior aspect of the flower (anterior/posterior line). Looking at the centre of the flower in the drawing the reader sees a side view and if the line of sight were produced through the flower it would travel through the lateral line

the anterior-posterior line and forming with it a St. George's cross (+) is the lateral line. These two lines may be regarded as four radii from the centre, each separated from the other by a right angle. When the flower is stalked and pendulous it should be turned into the upright position. The posterior aspect is that which morphologically makes the angle with the stem.

Bracts and Bracteoles

The individual flower arises in the axil of a comparatively unmodified leaf. This leaf may be suppressed, but its position must come at the base of the anterior aspect of the flower. A leaf which subtends a flower is known as a bract. One, sometimes two, similar leaves may arise on the actual flower-stalk, and these are termed *bracteoles*.

The Parts of a Flower

The Sepals

By reference to the circles and lines defined above, the position of any leaf in the flower may be located. Thus, in the flower of a cabbage, a kale, a wallflower, or any of their allies, four leaves

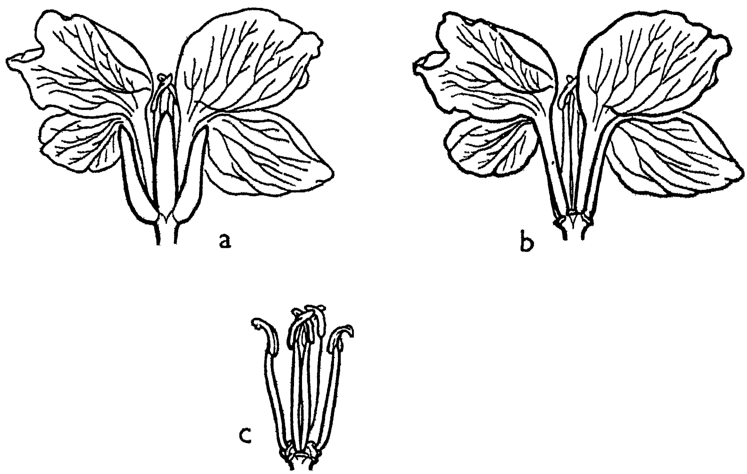


Fig. 57

Progressive steps in the dissection of a flower of the wallflower, turnip, shepherd's-purse family

(*a*) The intact flower (*b*) Sepals removed
(*c*) Petals removed (*d*) Stamens removed, and gynæceum exposed

(the sepals) are on the outermost circle. One of these is anterior, one posterior, and one on either side—that is, lateral. There are four regular sepals practically in one whorl. These leaves are referred to collectively as the *calyx*, and their function is to protect the flower.

The Petals

If the calyx of sepal leaves is pulled off, the insertion of four more leaves, the petals, is exposed. These are on a circle just inside that occupied by the sepals, and therefore lie nearer the centre. No petal, however, lies on the anterior-posterior line or on the lateral line, but all are on radii which alternate with those the sepals lie on. These four regular petals are said to be arranged in one whorl alternate with the sepals. The name applied to the petals as a group is the *corolla*.

The Stamens

Pulling off the petals exposes parts of a different form, the stamens. There are six of these : a pair of longer ones on the anterior position, a similar pair on the posterior position, and one short one on each of the two lateral radii. Thus the stamens lie on a circle within that of the petals, and on the same radii as the sepals. The stamens alternate with the petals. The stamens, being regarded as the male part of the flower, are known collectively as the *andrœcium*. Close examination of the insertion of the stamens may show that the two lateral members are inserted on a circle rather more remote from the centre than the one on which the anterior-posterior stamens are inserted, but this is a small point.

At the base of the two lateral stamens lie two green fleshy masses. These are organs for the production of nectar, and are called *nectaries*. Nectar, along with the colour of the petals, is known to attract insects to the flowers.

The Ovary

Removal of the stamens exposes a structure which occupies the central position, and which appears to be made up of one part only. The distal end, however, is bifurcate, suggesting a dual character. This suggestion is confirmed when the main body is

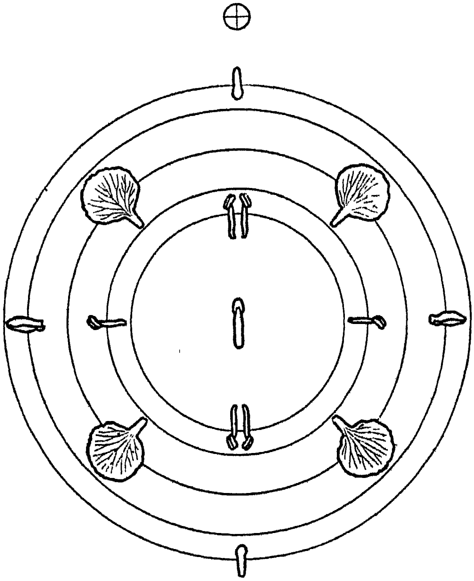


FIG. 58

The dissected flower parts laid out on a plane in the spatial relationships they occupied in the intact flower. Note that each set of leaves forms a cross. Plants with flowers of this type are crucifers

cut across (T.S.) at about its mid-point, and it is found to be hollow with two double rows of little stalked bodies attached inside. The number of double rows of such stalked bodies indicates that a number of leaves, in this case two, have grown together to form the composite structure. These leaves are called *carpels*, and because they are regarded as the female part are called collectively the *gynæceum*. In wallflower, kale, turnip, and their relatives the gynæceum is of two carpels grown together.

The gynæceum in all flowers comprises three regions. The top for the reception of pollen is the *stigma*, the column below it is the *style*, while the whole hollow " box " is the *ovary*. The little stalked bodies inside the ovary were at one time regarded as being eggs, and hence they are called *ovules*.

Sepals, petals, stamens, and carpels can each be regarded as leaves modified for special purposes, not so much modified in the sepal and petal, but considerably modified in the stamen and carpel.

⊕

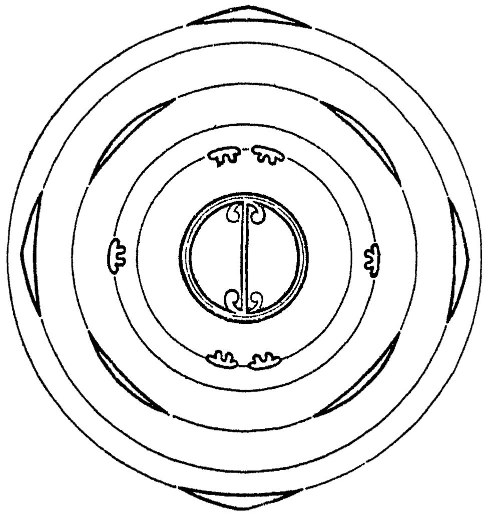


FIG. 59

Floral diagram of Fig. 58, showing the standard symbols used. ⊕ represents the axis of inflorescence

THE FLORAL DIAGRAM AND VERTICAL SECTION

A representation of the spatial relationship of these parts on a plane surface similar to a map is now possible. This is called the floral diagram. A map of a parish or of a country on a plane surface does not give the rise and fall of the land, and a contour map or section is required. A floral diagram must be supplemented with a representation of the parts as seen in a median vertical section; that is, a vertical section in the plane of the anterior-posterior line. In such a section of a wallflower the gynæceum appears inserted on the top of a small club, or knob-shaped ending of the flower stalk, the torus. The stamens, petals, and sepals are inserted about it in descending order.

Hypogyny

The ovary in this case, because it is inserted on the torus above all the other parts, is said to be *superior* in its insertion, or simply a superior ovary. Conversely, the flower parts being placed below the insertion of the gynæceum are said to be hypogynous, and the condition is known as hypogyny.

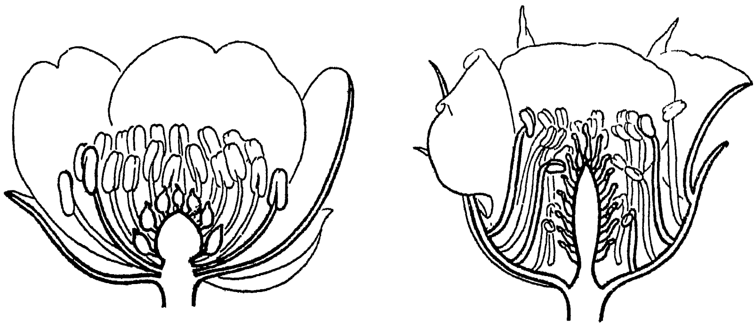


FIG. 60

Left Hypogyny (in buttercup). The many free carpels are inserted on the knob-like torus *above* the insertion of the stamens, etc.

Right Perigyny (in geum). The torus is saucer-like and the stamens are inserted at a level round about the insertion of the many free carpels

Perigyny

In some flowers—for example, that of geum or prunus—the torus has modified and extends out into a saucer-like form. The sepals, petals, and stamens are carried on to the lip of the saucer, with the gynæceum remaining inserted centrally in the bottom. In this way, to some extent, the ovary is better protected. The ovary is still described as superior, but as the other parts are now nearly at the same level, and disposed round and about the gynæceum, the flower is said to be perigynous, and this is the condition of perigyny.

Epigyny

The apple is related to the strawberry, but in it the process of toral modification has gone further, and has developed so far that it is now not saucer-shaped but cup-shaped. The ovary is inserted at the bottom of the cup and well protected by occlusion within the hollow torus. The sepals, petals, and stamens are inserted on the lip of the cup at a level above the ovary. An ovary sunk in a torus-cup with the sepals, petals, and stamens inserted above it is said to be inferior ; the parts being above the gynæceum, the condition is one of epigyny.

A series of flowers from different kinds of plants might be assembled to show a gradual progression from extreme hypogyny to extreme epigyny, and so represent a progressive evolution towards better protection of the ovary with its contained ovules.

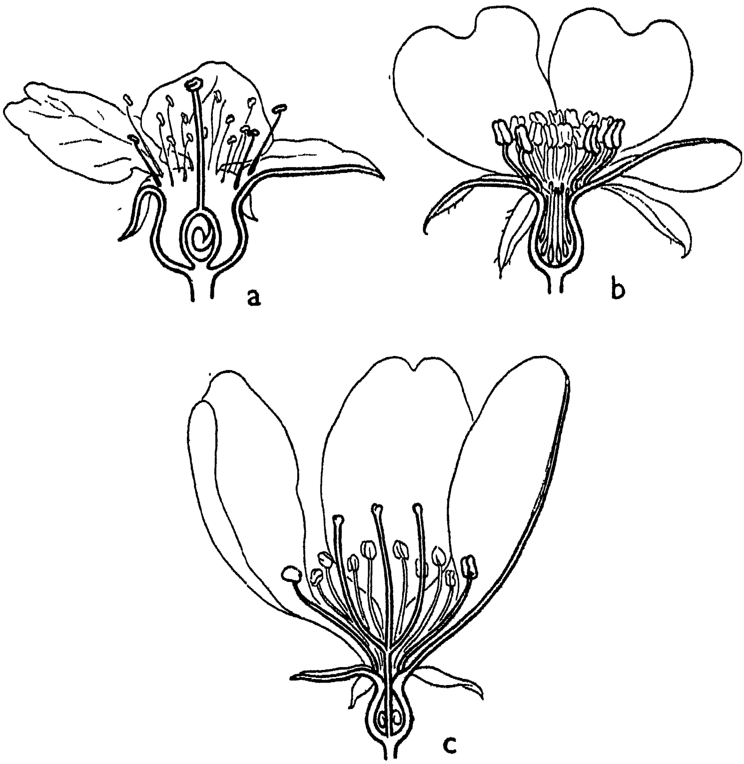


Fig. 61

(*a*) Perigyny in prunus ; (*b*) perigyny in rose, carpels free in torus cup ; (*c*) epigyny in apple, carpels and torus adherent

Irregular Flowers

The flower of a pea or bean or one of their relatives will show a partially irregular flower. There are five small regular sepals in the outermost whorl, and five petals in the next whorl. Of these the one in the posterior position is easily the largest, the two lateral petals are small, while two still smaller are grown together at their margins to form a keel-shaped structure. The stamens of the pea family are partially grown together, due to their stalks adhering while their heads remain free. Depending on which member of the family is chosen, there will be nine stamens grown together and one quite free, or all ten may be grown together.

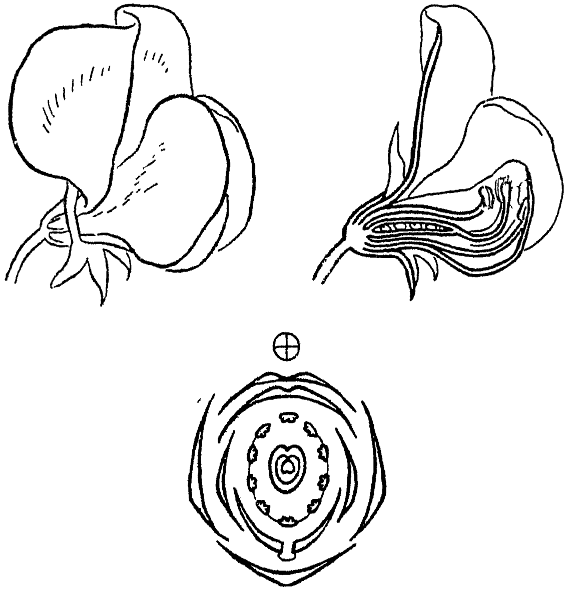


FIG. 62

The flower of the pea

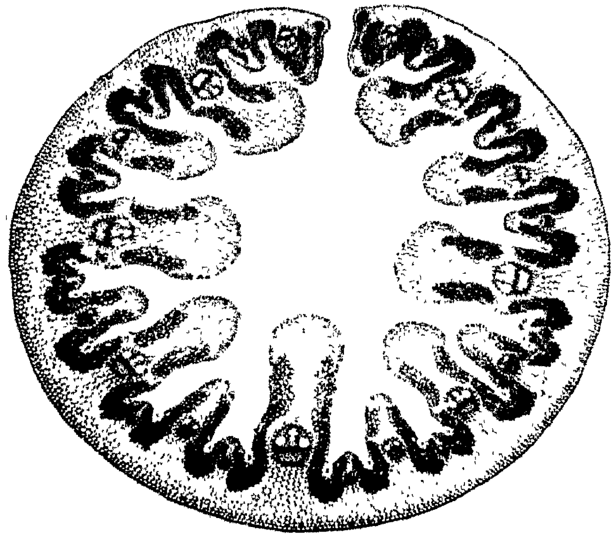
The ovary of this flower encloses only one double line of ovules. From this it may be deduced that this gynæceum has developed from one carpel grown together at its margins.

DIFFERENT KINDS OF OVARY

The ovary of the higher flowering plants, no matter how many carpels may be involved, is always a closed hollow box with no openings to the exterior. It may be made from one, or more than one, carpel.

Some flowers show more than one carpel, and these remain free from their neighbours. They do not grow together into one structure as do the two carpels of wallflower, but each forms a separate ovary by uniting at its two margins in the same way as the single carpel of the pea does. This condition is seen in the gynæceum of buttercup where there are as many separate ovaries as there are carpels, all free on a knob-like torus. When a gynæceum is composed of more than one carpel all free, it is

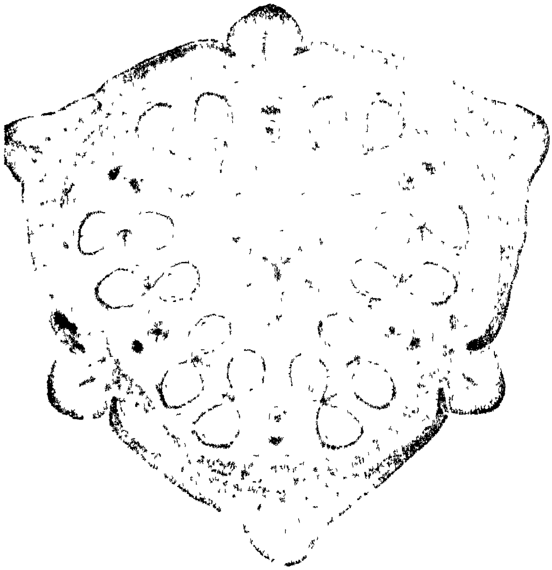
COLOUR PLATE XI
T.S. OF LEAF-BLADE OF MARRAM GRASS

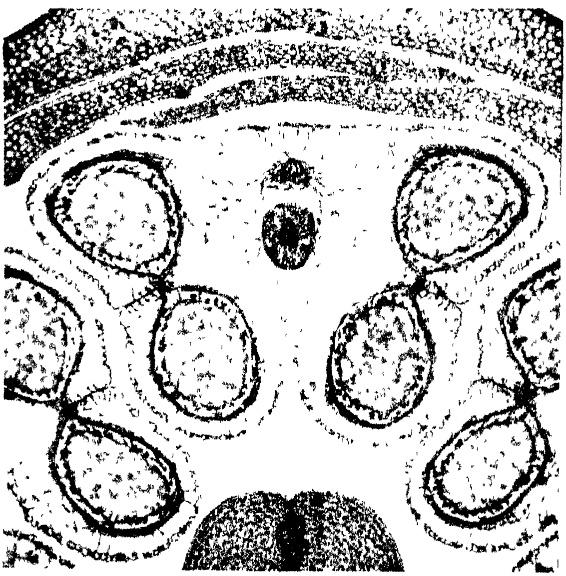


This blade shows extreme ridging of the upper surface. Motor tissue is located at the bottom of the furrows and stomata on the sides of the ridges. In dry air the cells of the motor tissue shrink and the blade forms a tube with the stomata inside. This aids control of transpiration. The blue-stained areas mark where the chlorophyll-containing cells lie. The pink-stained area is composed of cells more or less sclerenchymatous in character.

There is a vascular bundle in each ridge

COLOUR PLATE XII





COLOUR PLATE XII

FLOWER STRUCTURE

Upper: Transverse section of a flower bud of monocotyledonous type cut at the level of the anthers. Axis of inflorescence towards top of page

On the outside there are three sepals ; inside these and on alternate radii there are three petals. There are six stamens, three outer ones on the same radii as the sepals and three inner ones on the same radii as the petals. Centrally lies the gynaeceum. In each anther there are four lobes or sporangia, each filled with yellow pollen. No ovules appear in the gynaeceum, as the cut was made in the region of the style above the level of the ovary

Lower: A single anther under higher magnification

Centrally the pink-stained stalk or filament is seen. To right and left there are two sporangia each full of yellow pollen. Between the members of each pair of sporangia is seen a more deeply stained line of weakness—the dehiscence line. Each sporangium is lined with disintegrating cells which form a layer—the nutritive layer—supplying food to the developing pollen. Outside this is a layer of cubical cells—the mechanical layer. Externally the epidermis is seen. The mechanical layer when fully developed and dry will contract powerfully, tearing the anther apart at the dehiscence lines and so setting free the pollen

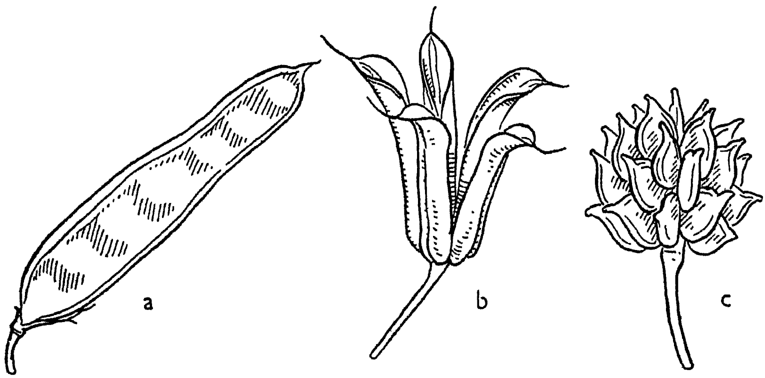


FIG. 63

Apocarpus gynæcia

(*a*) Pea (one carpel) ; (*b*) columbine (five carpels) ; (*c*) buttercup (many carpels)

said to be *apocarpous* ; when it is formed of a number of united carpels it is said to be *syncarpous*.

THE FLORAL FORMULA

The floral diagram and median vertical section of a flower together provide much information regarding it. The greater part of the data may be summarized in the floral formula. This

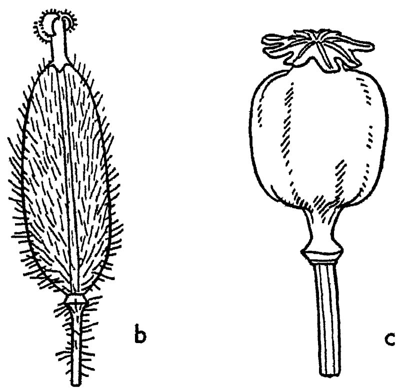


FIG. 64

Syncarpous gynæcia

(*a*) Willow-herb (four carpels) ; (*b*) blue poppy (four or five carpels) ; (*c*) common poppy (many carpels)

is a short statement consisting of symbols and numbers. The symbols in common use are: ✻ = regular, $\surd$ = irregular; Ca = calyx of sepal leaves; Co = corolla of petal leaves; And = andrœcium of stamen leaves; and Gn = gynæceum of carpel leaves. Numbers are used to indicate how many leaves are in each whorl. Brackets ( ) round any number shows that the individual leaves so enclosed are grown together. Finally, a horizontal line placed above or below the number of carpels shows the level at which the other flower parts are inserted. A line below the carpels indicates a superior ovary, while the line above indicates the inferior condition. The floral formula of wall-flower thus becomes ✻ Ca 4 Co 4 And 6 Gn $(\underline{2})$, while that of pea is ✻ Ca 5 Co (2) + 3 And (9) + 1 Gn $\underline{1}$. The data shown in the formula are constant for the flowers of any particular kind of plant, but will vary in any or every feature as between different species.

Abnormal Flowers

Aberrations may be found in the flowers in a particular kind, more especially those which have been subjected to intense cultivation. For example, the wild rose, typically, has five petals, but varieties with many petals and few or no stamens (double flowers) are well known to gardeners.

Flowers of plants belonging to the class dicotyledon typically have the flower parts in fours or fives or multiples of these numbers, while monocotyledons have the flower parts always in threes or multiples of three.

The Function of the Different Flower Parts

The sepals and petals (collectively the *perianth*), though often showing features of considerable interest and importance in classification, may be dismissed at this point with little further attention. The leaves of prime importance are the stamens and carpels. These are the so-called sexual organs. This appellation is true only in so far as the gametes or sex cells which fuse in the sexual act are formed deep within them.

In plants a gamete is always contained within a spore. In the flowering plants the spores are produced and nurtured within completely enclosed structures. A closed sac or box containing spores is called a *sporangium*.

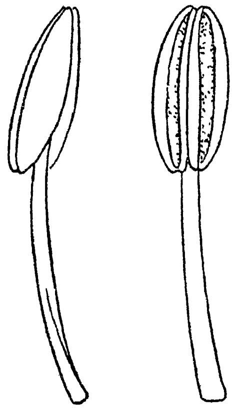


FIG. 65

Left The nearly ripe stamen showing stalk and anther

Right The same after a longitudinal split has torn open the lobes of the anther and exposed the pollen (dehiscence)

The Stamen

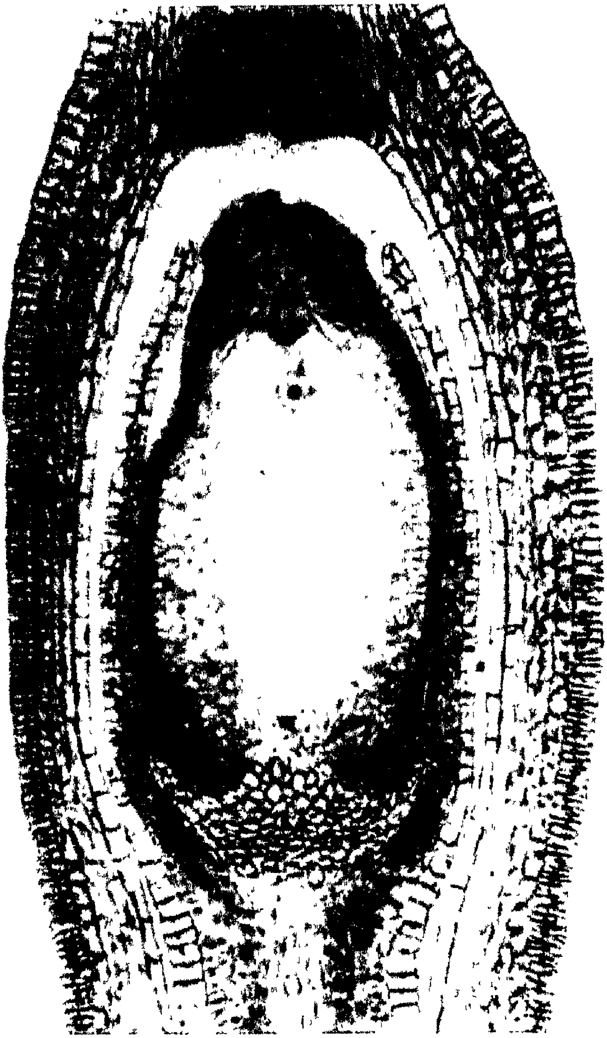
The stamen consists of two parts : the stalk or *filament* and a head or *anther*. The anther is a four-lobed structure, each lobe being hollow. Within each of the anther lobes many small spores, the pollen grains, are produced. The anther then comprises four sporangia. These sporangia ultimately burst to allow the spores to escape and complete their function.

The Gynæceum and its Parts

The gynæceum, whether of many carpels or of one carpel leaf, comprises three regions : stigma, style, and ovary. The ovary contains one or more ovules, and each ovule contains one large spore, which remains *in situ* to complete its function. The ovule is a sporangium.

Summary of Terminology

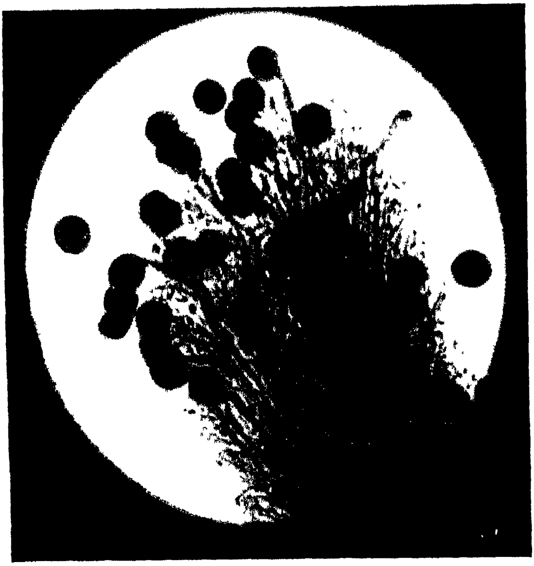
Two terminologies exist for the two kinds of gametes and the parts which produce them. The older terminology is somewhat complex but probably more familiar. The new terminology is standardized to show the relationship involved, and is therefore an aid to clear thinking. The prefix " micro " indicates the small " male " gametes or the parts connected with them, while the prefix " mega " serves for the large " female " gamete and its associated parts.



L.S. of an ovary containing one ovule

The ovary wall encloses the cavity containing the single erect ovule, which is borne on a very short stalk. The outer integument stands out from the inner integument, which is pressed against the body of the ovule. The upper tip of the inner integument is rather fleshy and forms the micropyle

The embryo-sac lies centrally, immersed in the nucellus. Inside the embryo-sac proximal to the micropyle the fertilized macrogamete is to be seen



Pollen grains germinating on a stigma

Immature embryo-sac—four-nuclear stage

Mature embryo-sac ready for fertilization

The two terminologies are tabulated side by side :

microgamete (generative nucleus)	megagamete (ovum)
microspore (pollen-grain)	megaspore (embryo-sac)
microsporangium (anther-lobe)	megasporangium (ovule)
microsporophyll (stamen)	megasporophyll (carpel)

Both terminologies will be used here in order to provide familiarity with the use of the various terms.

The features of prime importance are the micro- and megaspores with their contents, particularly the gamete. It is of considerable importance to understand how both are formed. The production of microspores in a flowering plant is a somewhat complicated process, but when the description is reduced to essentials the matter is comparatively simple.

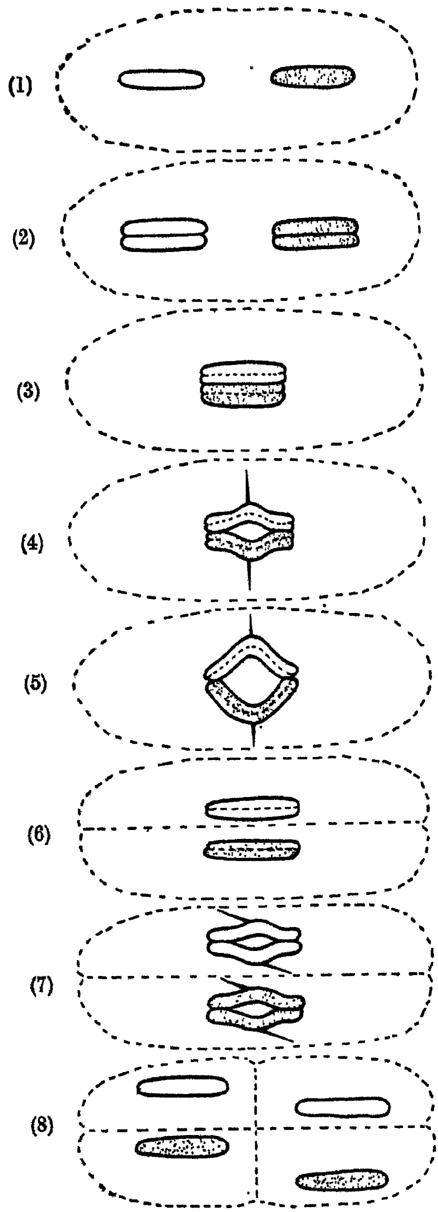
The Formation of Microspores (Pollen-grains)

Inside the anther lobe (microsporangium) a tissue of cells is built up until the whole cavity is filled. These cells are the microspore mother-cells. Each mother-cell will produce four microspores. To do this the nucleus of each mother-cell divides in a peculiar way.

Meiotic Cell-division

The chromosomes take form just as they do as a prelude to mitosis, but in this case members of homologous pairs are twisted round each other, or are at least in very intimate contact. This stage, with homologues in intimate contact, is called *syndesis*, and will be referred to later. The pairs arrange themselves on the equatorial plate. As in mitotic cell-division, each chromosome is split lengthwise into two equal portions. *Before the half-chromosomes produced by this split can part company* the " fibres " from the poles of the cell attach themselves to the chromosome. One fibre from one pole goes to one split chromosome of each pair, and a fibre from the opposite pole goes to the other split homologue. The fibres contract, each pulling its attached chromosome to the appropriate pole. Two daughter nuclei are so formed, one at either pole of the spore mother-cell. Each daughter nucleus contains *one* split *representatative from each* pair of homologous chromosomes. As soon as the two groups of individual chromosomes have congregated at the poles each one then completes its

Fig. 66



(1) The original cell

(2) The chromosomes show the start of the split

(3) The homologues associate in pairs (*syndesis*)

(4 & 5) The homologues part company

(6) The homologues separated in different cells

(7) The split halves of chromosomes part

(8) The tetrad is formed: Two of the four supplied from one member of the pair and the other two from the other member

Meiosis: Diagram to show what happens to one of the pairs of chromosomes (crossing-over omitted)

split. Another set of " fibres " reaches out from daughter poles and pull apart the now completely separate halves. Thus, from every spore-mother-cell four daughter nuclei, each with attendant protoplasm, are formed, and cell walls appear between the four. The individual cells round off and separate to give four spherical pollen-grains, each lying free in the microsporangium.

The important point to notice is that the nucleus in each microspore contains *only one member of each of the homologous pairs* of chromosomes seen in the nuclei of the body cells. In each spore nucleus there is a reduction of the pairs to individuals, and a reduction of the total number of chromosomes present to half.

The first division of the process is called reduction division, and the whole process of two divisions is called meiosis.

Meiosis may be summed up by saying it consists of two divisions of the nucleus with only one division of the individual chromosomes.

Any nucleus like those found in these microspores having a complement of single unpaired chromosomes is said to be haploid. The total number of chromosomes present in such a nucleus is the haploid number, and is usually indicated by the letter " n." The somatic nucleus with chromosomes in pairs is said to be diploid, and the total number in the complement indicated by " 2n."

All subsequent divisions of the haploid nucleus are mitotic. A nucleus with the reduced number cannot be further reduced ; *meiosis takes place only once in any life cycle.* The union of two haploid gametes at fertilization reconstitutes the diploid nucleus. Two phases may be recognized in a complete life cycle of a plant. One, the haploid phase, with nuclei having n chromosomes alternating with the other or diploid 2n phase. Put otherwise, the vegetative, diploid (2n), spore-producing, sporophytic phase gives rise to the reproductive, haploid (n), gamete-producing, gametophytic phase which in turn following union of the gametes reconstitutes the soma.

Maturation of the Pollen-grain

Let us return to consideration of the newly formed microspore with its haploid nucleus immersed in protoplasm, within a thin cell wall, and trace its further history. The single nucleus divides mitotically ; the chromosomes split longitudinally, one-half from each goes off to one pole, and the other to the other pole. Two

nuclei form. No cell wall appears between. At this stage the microspore is mature and binucleate. The two nuclei look alike, but one is all-important and called the generative nucleus ; the other is of minor importance, and is called the vegetative nucleus.

While the spore is in this condition and nourished within the anther-lobe its wall alters. It becomes thickened by an external layer, which has little thin spots or pores in it. The original thin cellulose inner wall is called the *intine*, while the thick outer wall with pores is called the *extine*. The ripe microspore or pollen-grain may now be described as a free, one-chambered, binucleate body, richly supplied with protoplasm, with a double wall.

The Megasporangium

The ovule, to which attention should now be turned, is a small oval or egg-shaped structure borne on a short stalk called the funicle. This stalk is attached at its other end to a thick mass of tissue on the internal wall of the ovary called the *placenta*. A median longitudinal section of the ovule shows that it possesses two coats, the inner integument and the outer integument. These invest a central mass of tissue called the *nucellus*. The two integuments are not quite entire, for a small canal, the micropyle, is left at the end distal to the funicle.

The Megaspore

As the ovule develops, *one* of the cells of the nucellus, the megaspore mother-cell, enlarges and its nucleus divides meiotically.

In short, deep in the nucellar tissue four cells are produced, each with a cell wall enclosing protoplasm and a haploid nucleus. These are megaspores. Three of the megaspores in the tetrad die and are absorbed ; the other one persists and enlarges. This large, thin-walled haploid cell lying imbedded in nutritive tissue, protected by integuments and further protected by the ovary wall, is the megaspore or *embryo-sac*. Any further divisions of the nucleus of this cell must provide only nuclei, each with the half number (n) of chromosomes.

Maturation of the Megaspore

The nucleus does divide to give two such nuclei. On formation these migrate, one to the end of the embryo-sac nearest the micropyle, and the other to the opposite extreme or antipodes.

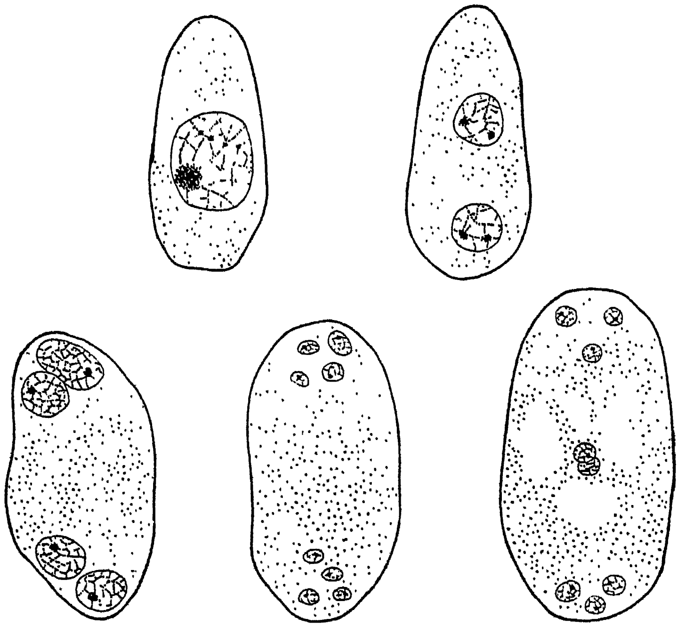


FIG. 67

The maturation of the embryo-sac

The embryo-sac when formed by meiosis has one nucleus. Eventually it comes to contain six nuclei (each with n chromosomes) and one double nucleus ($n + n$ chromosomes)

No cell-wall appears between them. Each of these two nuclei lying at the remote ends of the spore then divides and re-divides, so that the embryo-sac comes to contain eight nuclei, four at each end and all haploid. One nucleus from each group of four now migrates towards the centre of the spore. There they meet and fuse to give a centrally placed fusion-nucleus. The embryo-sac is now mature.

At the end of the sac nearest to the micropyle lie three nuclei, all of very similar appearance. One of these is the all-important megagamete or *ovum*; the other two are of very minor importance, and are called the "help-cells" or synergids. At the end of the embryo-sac farthest away from the micropyle lie three other nuclei of similar appearance, all of ephemeral function and called the antipodal cells. In the centre lies the central-fusion nucleus, formed from two nuclei and therefore diploid, which has a function second only to that of the gamete itself.

The Ripe Spores

The position now is that ripe, single-chambered pollen-grains, each with a vegetative and a generative nucleus, are set free to the outer world by the bursting of the stamen. At the same time lying deep in the nucellar tissue of an ovule enclosed in the ovary, are single, one-chambered megaspores, each containing one megagamete, one central-fusion nucleus, and five other nuclei.

POLLINATION

The further history of the microspore can now be followed. After the anther lobes burst or dehisce, the pollen is set free and is carried by some agent such as wind or an insect from the stamen to the stigma of the gynæceum. The stigmatic surface at this stage is wet with exuded sugar solution. The sugar solution causes two changes in the pollen-grain. Firstly, the generative nucleus becomes active and divides into two nuclei, both generative in function. The other nucleus (vegetative) remains undivided, and is merely for the physiological control of the spore as a whole.

The two important members are called the first and second generative or male nuclei.

Pollen Germination

Concurrent with these changes the liquid contents of the pollen-grain increase and cause the intine to " blister out " where it is not rigidly supported by the extine—that is, at one or other of the pores. The intine, being pressed out through this narrow orifice, forms a narrow-bore, thin-walled tube. This is the pollen tube. Into the tube so formed passes the vegetative nucleus which controls the physiology of the whole structure. The pollen tube steadily elongates and passes down through the tissues of the stigma, style, and ovary to the level of the ovules. Here the tip grows in the direction of the micropyle of an ovule. The micropyle is entered, and the tip of the tube passes up into the nucellus, lying between the micropyle and the embryo-sac. While all this has been going on, the two generative nuclei have entered the tube and followed the vegetative nucleus into its tip.

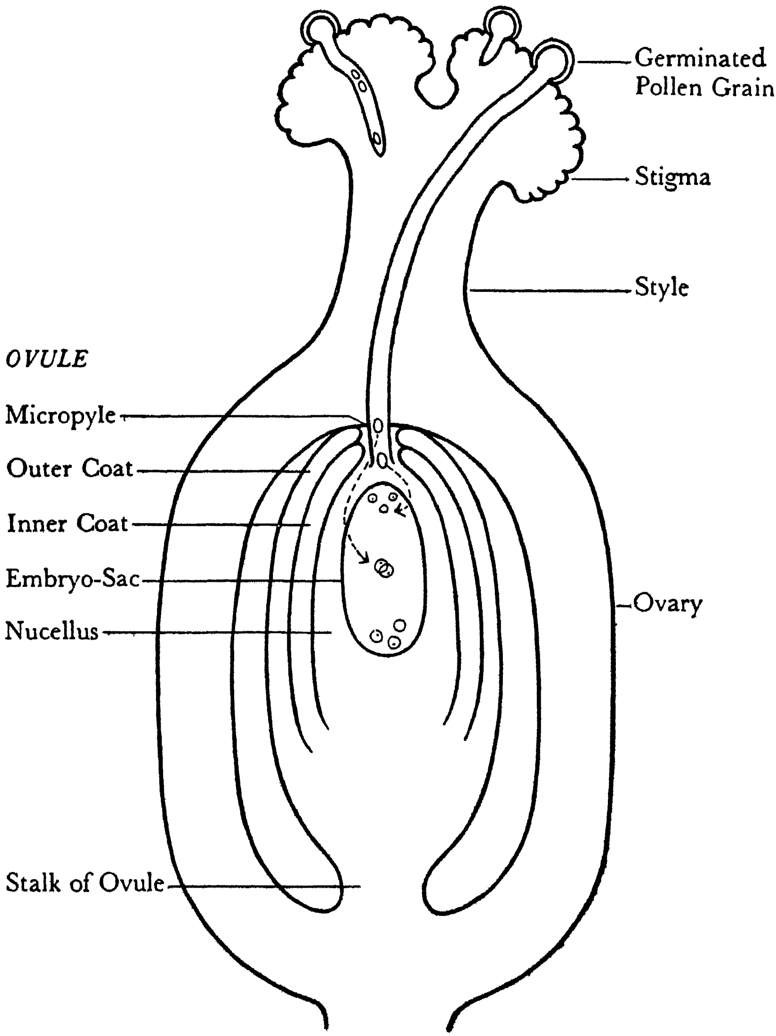


FIG. 68

The gynæceum at the moment of fertilization

Fertilization

When the tip of the tube reaches the embryo-sac the vegetative nucleus, its function completed, is absorbed, and so disappears. Now the wall of the tube at its tip breaks down or bursts,

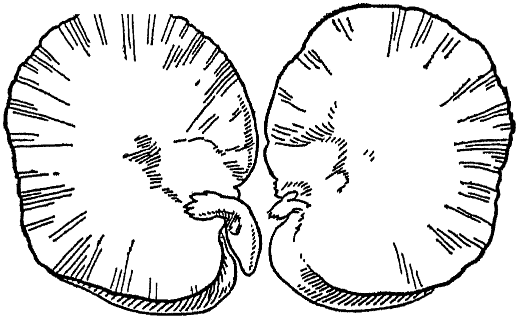


FIG. 69

The dicotyledon embryo

The two massive cotyledons (split apart in drawing) contain a reserve of food for the future development of the plumule and radicle seen attached to the left-hand cotyledon. In this seed (the bean) the endosperm is all absorbed early, it is non-endospermic

and the two generative nuclei flow up and enter into the embryo-sac. One fuses with the megagamete and the other with the central-fusion nucleus. This is the sexual act or act of fertilization.

There are now two nuclei present in the embryo-sac, each with more than the n number of chromosomes. One is the fertilized megagamete or ovum, which is 2n, now called the *zygote*, and from which by mitotic division the embryo and the new plant develop. The other is the central-fusion nucleus plus the second generative nucleus. This unit, derived from *three* haploid nuclei, is 3n, or triploid.

ENDOSPERM

By a series of divisions all more or less aberrant, this triploid nucleus produces daughter-cells of various chromosome numbers, and a tissue called endosperm is built up. The endosperm fills that part of the cavity of the embryo-sac not occupied by the embryo itself. Endosperm is purely temporary in character, and is produced only for the nutrition of the embryo, which sooner or later absorbs it.

The whole of these processes may be shown summarized in tabular form. The arrows in the table can be interpreted as meaning either " produces " or " contains."

SUMMARIZED HISTORY OF THE STRUCTURES AND PROCESSES INVOLVED IN THE PRODUCTION OF GAMETES AND THEIR UNION TO FORM A NEW GENERATION

VEGETATIVE PLANT: SOMA (2n)

Male side

Microsporophyll (stamen) ↓ Microsporangium (anther lobe) ↓ Microspore mother-cell (pollen m.c.) — 2n

↓

MEIOSIS

↓

4 Microspores (pollen tetrad)
↓
Separate microspores (pollen grains)
↓
Microspore nucleus divides to give two, the generative and vegetative nuclei of the spore
↓
Microsporangium bursts and spores are set free
↓
Microspores transferred from stamen to stigma of gynæceum. Pollination
↓
Spore germinates to form a tube; generative nucleus divides into first and second generative nuclei
↓
First generative nucleus in tube | Second generative nucleus behind it — n

Tube reaches micropyle and bursts

↓

First generative nucleus } Enters megaspore { Second generative nucleus

Female side

Megasporophyll (carpel) ↓ Megasporangium (ovule) ↓ Megaspore mc (embryo-sac mc)—a cell of the nucellus — 2n

↓

MEIOSIS

↓

4 Megaspores in tetrad (putative embryo-sacs)
↓
3 absorbed leaving one megaspore (embryo-sac)
↓
Single unicellular megaspore buried in nucellus
↓
Nucleus divides: daughter nuclei migrate to poles of spores
↓
Division and redivision produces two groups of four cells, one group at each end of spore
↓
One from each group migrates to central position and there they fuse. This gives three groups of nuclei in the spore
↓
Central fusion nucleus (2n) | Mega-gamete | 2 synergids | Antipodal cells — n

2 synergids, Antipodal cells ↓ Ultimately absorbed after fertilization

Fertilization

Second generative nucleus + Central fusion nucleus ↓ Fusion to provide endosperm nucleus which divides ↓ Endosperm a temporary tissue later absorbed — 3n

First generative nucleus + Mega-gamete ↓ Fusion to provide zygote which divides repeatedly

↓

Embryo and new generation

↓

Vegetative phase — 2n

Cross- and Self-pollination

A necessary incident in the processes just described is the transfer of microspores from the microsporangium to the stigma. The transfer is called pollination. A flower, once it has received pollen, is said to be pollinated. The move may be from the stamens of a plant to its own stigmas. In this case the plant or flower is said to be self-pollinated or selfed. If pollen from another plant is brought in, cross-pollination is said to have been effected, or the plant crossed. There are various degrees of each. One flower or two separate flowers on one plant may be involved in self-pollination.

Other things being equal, cross-pollination seems to be preferable to selfing, for usually the offspring are stronger and more robust. Also, in later generations the progeny of a cross show a higher degree of variation for selection to work on.

The Natural Agents of Pollination

The natural agents for carrying pollen are, most commonly, either wind or an insect. Plants normally wind-pollinated have small, insignificant, dull flowers, devoid of colour or scent. The pollen produced by these flowers is dry and dust-like. The stigma is usually a much branched feather-like organ apt to catch drifting pollen. The stamens have long stalks, and are usually so constructed as to shake the spores freely out on the wind.

Flowers adapted for insect pollination, on the contrary, are usually bright-coloured, scented, and nectar-producing. They are attractive to insects. The stamens are not adapted to scattering the pollen, which tends to be sticky. Often the construction of the flower is specially adapted to facilitate the entrance of a particular kind of insect, or to guide it in such a track as will increase the chances of cross-pollination.

Successful pollination leads on to fertilization and the formation of an embryo. Many other changes flow from these acts, for the ovule as a whole is stimulated to develop and form a seed. A seed is a whole, ripened ovule after fertilization of the contained gamete. The ovary, too, is stimulated to grow and alter so as to produce a fruit. A fruit is a whole ripened ovary after fertilization. Other parts—torus, perianth members, style, and stigma—may also be stimulated to make structures necessary in the future of the fruit or seed.

False Fruiting

Pollination itself, though fertilization fail, may be a stimulus to development of secondary structures and fruiting without seed-formation results. This is seen in such cases as the seedless raisin, the banana, the seedless orange, and so on. False fruiting of this type is not uncommon; the plants showing it are said to be fruitful but sterile. The causes underlying sterility will be discussed in Section Four.

THE DEVELOPMENT OF THE ZYGOTE

The normal sequel to effective fertilization is that the zygote divides mitotically into two, and then into four. Each of these cells by continuous division produces a small embryo plant lying enclosed within the altered or altering ovule. The embryo consists of a very short axis, with one end, the root-to-be, called the radicle, pointing towards the micropyle. At the opposite end of the embryo axis is a small portion, the shoot-to-be. This terminates in a very elementary bud which looks like a little feather. The early botanists called this embryo terminal bud the plumule. Midway between the radicle and plumule is inserted either one or two embryonical leaves, the cotyledon leaves.

The Embryo

The embryo then consists of plumule, radicle, and cotyledon(s). The cells composing the various tissues are not greatly developed at this stage, and all might be described as meristematic in character. They are filled with protoplasm, which, as has been said, is nearly pure protein. This accumulation of protein in the formation of the embryo, while it provides man with sources of valuable food, puts a considerable strain on the mother plant.

After the various tissues have developed and reserves of food placed in position, the seed with its contained embryo will be detached from the mother plant and transferred to the soil. From then on it will have an independent existence. Before it is ready to manufacture food for itself and become self-supporting, it will have to send the root into the soil and the shoot above ground to develop leaves. It must grow. Provision of a sufficient supply of food must be laid down in the seed for these future needs.

Food Reserves in Seeds

In some seeds a remnant of the nucellus persists into the seed stage and may help to supply this need. Such a reserve is called *perisperm*. In most cases, however, perisperm would be quite inadequate and other methods have been adopted. Rapid divisions of the central-fusion-nucleus going on concurrently with embryo formation produce a mass of undifferentiated tissue. The cells of this tissue are filled with food from the mother plant and the reserve called the endosperm is built up. The fate of the endosperm is to be consumed by the embryo. In the seeds of some plants the endosperm persists as a massive tissue, and these seeds are described as endospermic. In others, however, the developing embryo absorbs the endosperm practically as it forms. Such a seed when ripe contains practically no endosperm. In these non-endospermic seeds the food is stored within the embryo usually in much-swollen cotyledons.

Changes in the Integuments

While all these changes are going on inside the one-time ovule, the integuments alter very considerably, becoming tougher, harder, and better developed to protect the embryo and its food reserves. Together, these coverings form the *seed-coat* or *testa*. This envelops the whole of the seed, and is pierced only by the micropyle.

The whole of the structure derived from the ovule progressively dehydrates, so that the water content falls. When this process of dehydration reaches a low point the seed is said to be harvest-ripe.

Dryness imposes a period of functional quiescence or cessation from activity. The dry quiescent structure is the resting seed.

Changes in the Ovary—Fruit Formation

While the ovule is undergoing these changes the ovary, too, is altering. The developments of the ovary follow as a result of pollination and fertilization. The changes in the ovary are generally designed to facilitate the distribution or dispersal of the seed. It is beneficial to any species when its seeds are carried as far away from the parent and as far away from each other

as may be possible. If a site suitable for their subsequent germination is automatically selected, this too is an aid. Hence, the evolutionary modifications seen in the fruit are almost all designed to ensure that a single seed, or a one-seeded fruit, or a one-seeded part of a fruit, is the unit of dispersal. In addition, the modifications often show a degree of adaptation to the habits or character of some special agent which will carry the one-seeded unit to fresh fields. The agents most commonly involved are wind and animals. The animal may be a bird or a mammal.

Two main classes of fruits can be recognized : those which are hard and dry, and those which are soft and succulent. There are many beautiful modifications of fruits and seeds of both those types which adapt the parts for the act of dispersal by one or other of these agents.

Seed and Fruit Dispersal

The simplest case is seen when a multi-seeded fruit splits or opens to allow the seeds to escape. The act of opening is called *dehiscence.* The pea provides a well-known example of a dehiscent fruit. The pod derived from one carpel splits longitudinally by two valves. The turnips, kales, etc., split in much the same way.

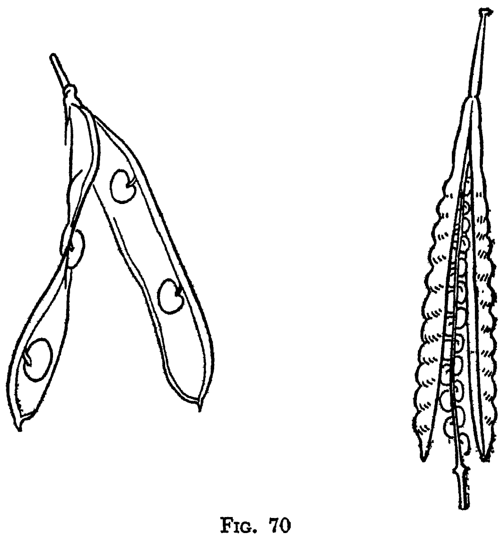


Fig. 70

Fruit dehiscence

Left pea type *Right* turnip

FIG. 71
Fruit dehiscence

Left Poppy dehiscing by pores
Right Willow-herb splits to allow the hairy seeds to blow away on the wind

though here two carpels are involved in the seed capsule. The wallflower fruit opens in exactly the same way, but the seeds are not round as in turnip and kale, but are flat and slightly winged, so that after the fruit opens they are borne some distance on the wind.

In the poppy, another multi-carpellary fruit, the apex of each individual carpel curls back and downwards to form small pores underneath the " eaves " formed by the segments of the persistent stigmas. As the poppy head on its tall stalk sways in the wind the small seeds are thrown out from the pores. This ensures release of the seeds only when a wind is blowing of sufficient strength to carry the small poppy seed some distance from the parent.

Adaptation to wind dispersal can be carried to a much higher stage of perfection. For example, in willow-herb, parachute-like hairs ensure the seeds being carried great distances after the multi-seeded fruit has split.

Splitting Fruits

Multi-seeded dry fruits which do not dehisce split into one-seeded parts. An excellent example is provided by seradella. This fruit is morphologically a pod similar to that of a pea. In it narrow " waists " appear transversely across the pod. When quite dry these divisions crack across, so splitting the pod into one-seeded parts. Runch, a near relative of the turnips and radishes, shows

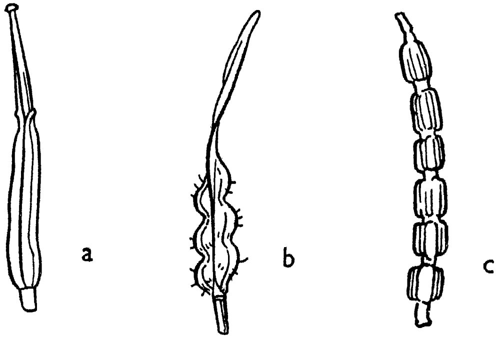


FIG. 72
Fruits of Crucifers

(*a*) The two-valved dehiscent fruit of charlock
(*b*) The two-valved dehiscent " waisted " fruit of white mustard
(*c*) The indehiscent waisted fruit of runch, which splits transversely into one-seeded parts

a somewhat similar mechanism. In carrot and its relatives the two carpels of the ovary separate, when ripe, into two one-seeded parts. Splitting fruits, then, are quite commonly met with, and are termed *schizocarpic.*

One-seeded Indehiscent Fruits

A one-seeded, entire fruit has been developed by some plants. An excellent example is black medick. This legume had at one time a multi-seeded, uni-carpellary pod much as is still seen in lucerne, or indeed in pea or bean. In black medick, however, the pod has become shorter, and only one ovule per pod reaches the mature seed stage. Normally, this one-seeded pod does not open. It is therefore classed as a one-seeded, dry, indehiscent fruit, though it clearly derives from a multi-seeded dehiscent pod. Any dry, indehiscent, one-seeded fruit, irrespective of its derivation in evolution, is called an *achene.*

The fruit wall, or pericarp as it is termed, may vary in character. For example, it may be woody as in hazel, and so form a nut. In a grass the pericarp is transparent and fused to the testa or seed coat. The grass fruit is an achene and its transparent pericarp is called a *caryopsis.* The caryopsis of wheat is a very typical example.

In many grasses the true fruit remains invested in one or

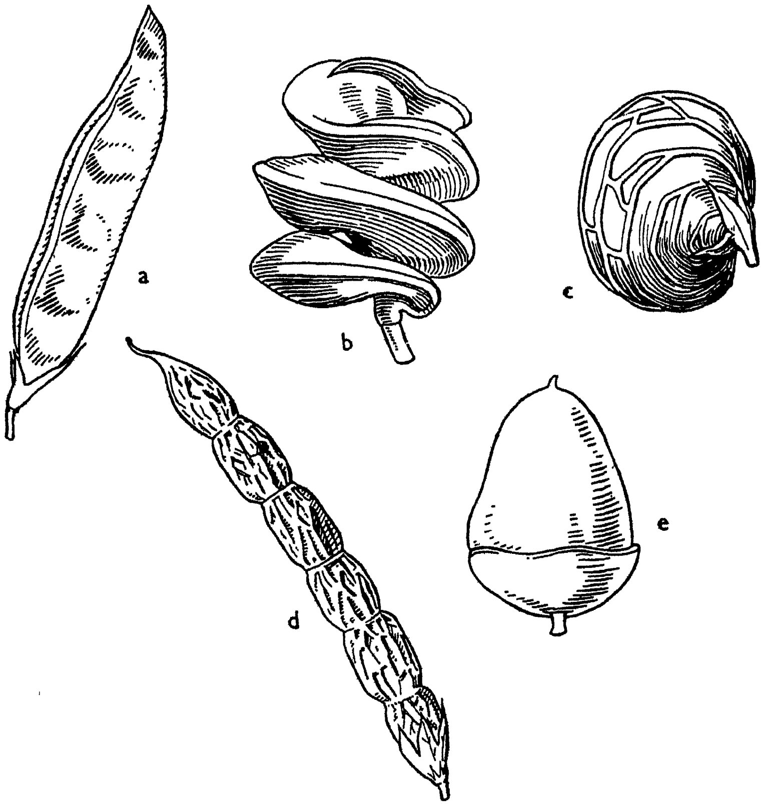


FIG. 73

Leguminous fruits

(*a*) The simplest type a straight pod (pea)
(*b*) The spiral pod (lucerne)
(*c*) The spiral one-seed pod (black medick)
(*d*) The straight pod splitting into one-seeded parts (seradella)
(*e*) The one-seeded pod splitting transversely to allow seed to escape (red clover)
(All are formed from one carpel)

more leaves not truly members of the flower parts. The oat grain provides an example of this. In most oat varieties the investing bracteoles do not leave the grain, though they may be stripped off by hand with more or less ease. In some peculiar varieties of oat the fruit escapes naturally from the leaves, and these kinds are known as naked oats or huskless oats. Normally, it is difficult to separate off the leaves investing the fruit of barley or rice, both of which are also cereal grasses.

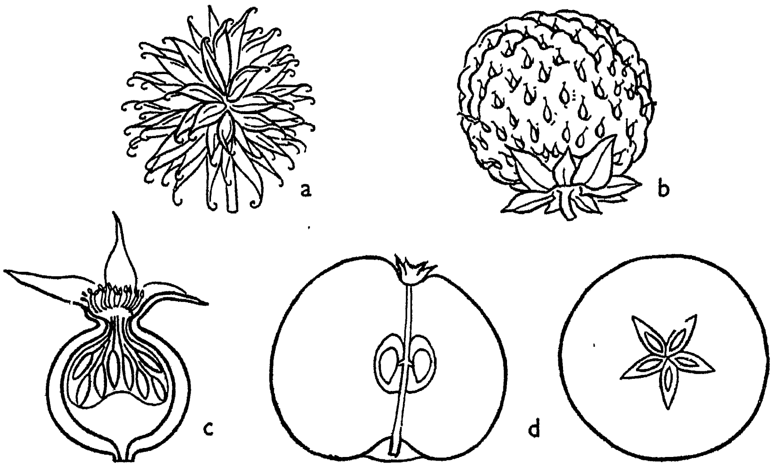


Fig. 74

(*a*) The dry achenes of avens (note hooked style)
(*b*) The achenes of strawberry on the fleshy development of the torus (note persistent calyx)
(*c*) The achenes of rose inside the fleshy cup-shaped torus (rose hip)
(*d*) The apple with its seeds inside the hard dry carpels, which are embedded deep in the fleshy development of the toral cup
Note persistent flower parts of strawberry, rose and apple

There are many other achene fruits; for example, that of avens, where the persistent style of each member of a multi-carpellary apocarpous gynæceum forms a hook for clinging to wool, etc. This provides for animal dispersal.

Another achene is seen in the strawberry. The true fruits, or "pips," are hard, dry indehiscent products of many one-seeded carpels. The succulence of the strawberry "fruit" derives entirely from a torus developed extraordinarily after fertilization. The persistent calyx or husk seen at the base of the "fruit" shows that the ovary was superior.

The rose shows a somewhat parallel development where extreme perigyny in the flower provides a degree of protection for the carpels, and later in the fruiting condition the torus provides an aid to animal dispersal of the achenes. The wall of the rose hip is torus and the "pips" inside are achenes. The persistent calyx at the neck of the toral cup is a clue to the nature of the structure.

The apple shows an even more advanced stage in evolution. In the flower the five-carpelled gynæceum with inferior ovary

sunk in a toral cup was well protected. After fertilization the torus develops considerably. The fleshy wall is torus ; the true fruit wall is the horny-like structure in the core, and the blackish pips are true seeds. The rose hip, the strawberry, and apple are " false fruits." The fleshy character, flavour, aroma, and bright colour of the ripe condition common to all these cases are all attractive to animals so that they eat the " fruit." The achenes or seeds after ingestion resist the digestive juices, and are later voided in the fæces.

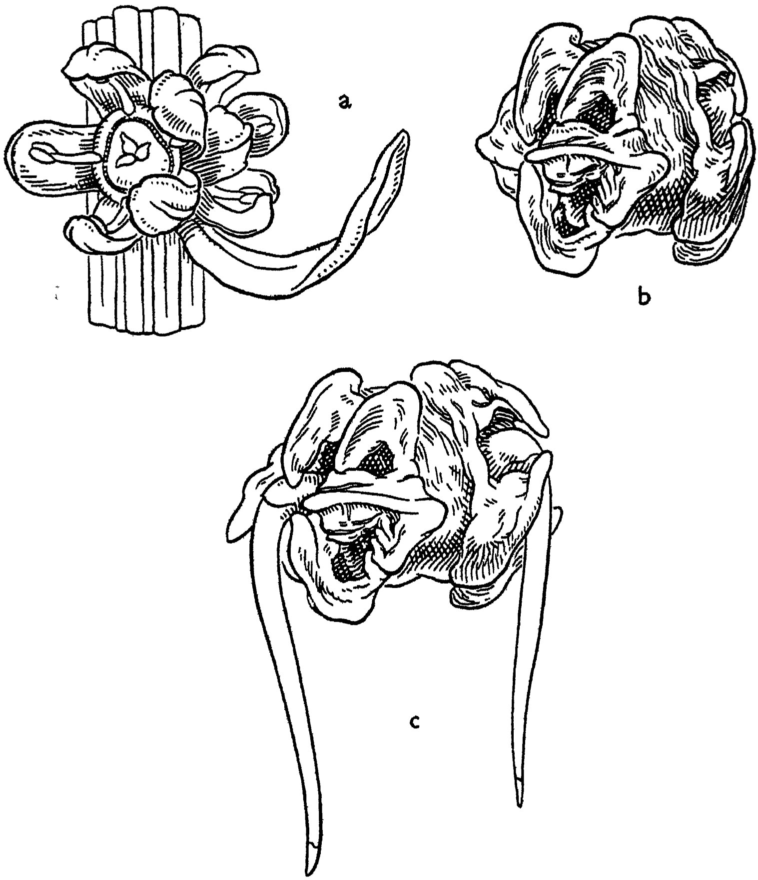


FIG. 75

The mangold " seed " (b) develops from a cluster of individual flowers (a), and on germination (c) a seedling comes from each of the one-seeded ovaries involved

Multiple Fruits

Another fruit seen in agriculture derived in a peculiar way is that of the mangold or beet. Both plants produce very many small, insignificant flowers grouped in small clusters of two, three, or more individual blossoms. Each flower has one carpel containing one ovule. After fertilization the calyces of these flowers develop considerably and grow together. A composite unit is formed from each cluster of flowers, and contains the ovaries of the two, three, or four flowers involved, all grown together by the now very hard, dry calyces. The so-called " seed " of mangold is a *multiple fruit*, the product of the ovaries of more than one flower. The small tips of the five sepal leaves of each flower remain free, and may easily be recognized in the dry seed cluster. The true fruit of the mangold is a small black body sunk deep in the tissues of the calyx. This adaptation is not useful in dispersal, rather the contrary, but is useful to the plant in germination.

The " seed " of mangold is a part of an inflorescence, the fig is a complete one. Each " pip " in a fig is an achene, while the fleshy wall is a highly modified axis of inflorescence. The pineapple of commerce too is a whole inflorescence in fruiting condition.

Apogamy and Parthenogenesis

Some plants after going through " all the motions " of spore production do not use the male and female gametes in the normal way. When one or other of the nuclei in the embryo-sac forms an embryo without fertilization parthenogenesis is said to take place. When a diploid nucleus of the nucellus produces an embryo plant the term *apogamy* is usually applied to the process. The ultimate seed produced by apogamy or parthenogenesis may be quite similar in appearance to one developed after fertilization. In effect parthenogenesis (and often apogamy too) is quite equivalent to vegetative propagation, for no sexual act has taken place.

Vivipary

In the flowering region of a number of plants (including a few grasses) a plantlet often appears in place of a normal seed or fruit. In some cases these plantlets arise as a proliferation of diploid

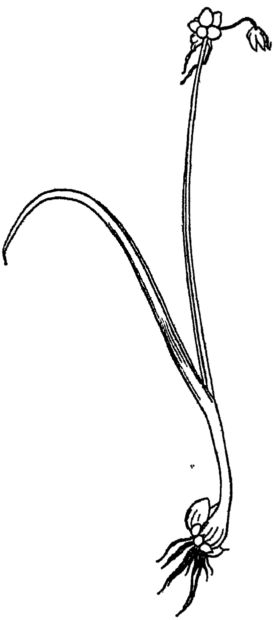


FIG. 76
Bulbils in the inflorescence of a plant related to onion: bulbs in the normal position

tissue, and constitute a form of vegetative propagation. The plantlet takes various forms. In some it resembles a normal seedling, in others it has all the characters of a bulb. Examples of the latter type are referred to as *bulbils*. No matter what the form, replacement of a fruit by a juvenile, but not purely embryonic structure, is called *vivipary*, and the plant showing it is said to be viviparous.

A simulation of vivipary often occurs when a true seed germinates before its release from the parent. This is commonly seen in cereals when the weather at harvest is warm and moist. The grain is said to "sprout in the stook." Cases of premature germination should not be referred to as vivipary.

The general facts outlined in this chapter enter into a great deal of the work of applied botany, and some examples of these will be offered in the next chapter.

BOOKS FOR FURTHER READING

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GUSTAFSON, T. G. "Parthenocarpy: Natural and Artificial" (*The Botanical Review*, 8 (9), 1942)

DARLINGTON, C. D. *Recent Advances in Cytology* (J. & A. Churchill, London, 1937)

BRIMBLE, L. J. F. *Flowers in Britain* (Macmillan, 1945)

JONES, S. G. *Introduction to Floral Mechanism* (Blackie, 1939)

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PLATE VIVIPARY IN A GRASS

Whole head

One spikelet

PLATE 42 THE GRASS SPIKELET

The spike-like panicle of Foxtail spread to show spikelets terminal on branches of the rachis

Spikelets of Meadow Grass. (*Left*) The unopened condition (*Right*) The flowering condition

Chapter VIII

SPECIAL ASPECTS OF THE INFLORESCENCE, FLOWER, FRUIT, AND SEED IN AGRICULTURE

To the botanist the greatest importance of the inflorescence, flower, fruit, and seed derives from their considerable use in identifying and classifying plants. Apart from that on the grasses, this class of work will be relegated to a special chapter, and at this stage consideration will be given rather to those cases where the reproductive system or its parts are the marketed or consumed portion of the plant.

The use, in this way, of any stage in the sequence from flower bud to ripe fruit can be illustrated by a series of examples taken from the many cases presented by world agriculture.

Cloves

The unopened flower buds of a particular tree come on the market as cloves. These are valued for the flavour and aroma with which an oil in their tissues is impregnated. The oil is sometimes extracted from the buds, and is marketed as clove oil for use as a flavouring agent or as a mild antiseptic.

Saffron

The stigmas and part of the styles of saffron, a kind of crocus, are harvested and marketed as a source of the dyestuff saffron. There are many examples of the whole flower or the petals of different plants being harvested for the production of oil, scent, cosmetics, dyes, and sweetmeats.

Cauliflower or Broccoli

The " curd " seen in cauliflower or broccoli is a large proliferated inflorescence developed as a storage organ in the first year of this biennial plant; in the second year normal flowers are produced from it.

Hops

The hop used in brewing and baking is a small mature inflorescence of somewhat peculiar structure and occurrence. The actual flowers of this plant are not hermaphrodite, *i.e.*, containing both stamens and carpels, but are unisexual. Any individual flower is either male (staminate) or female (pistillate).

When, as happens in some plants, both male and female flowers are borne on one plant, the condition is termed *monœcious*. When flowers of each of the two sexes are on separate plants, as in hop, the condition is described as *diœcious*.

In hop itself the male flowers are not of much importance in practice. They are borne on small, much-branched inflorescences which arise each in the axil of a leaf (bract) of the main or branch stems. A five-membered perianth is present. These leaves rather resemble sepals and may be referred to as the calyx ; if this

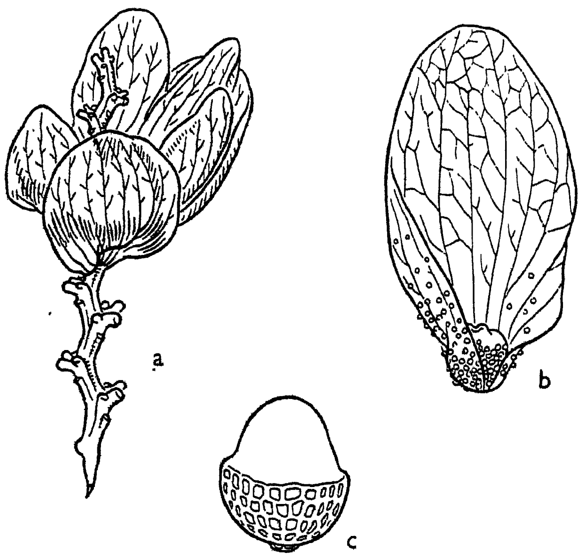


Fig. 77

(*a*) Dissection of a hop strobile or female inflorescence. Notice on lower part of main axis or strig the scars of attachment of the two stipular bracts and the stalks of four female flowers with their bracteoles. Above is seen a group of these leaves attached to right-hand side of strig

(*b*) One bracteole with seed and lupulin glands

(*c*) One lupulin gland magnified

is the case there is no corolla. The rather vague description of "sepaloid perianth" for this whorl commits the student to a less definite opinion. The andrœcium is of five stamens inserted on the same radii as the perianth members. As has been said, there are no carpels.

The Hop of Commerce

The inflorescence which bears female flowers, when mature, is the hop of commerce. Each little inflorescence or individual hop, called in practice a strobile, arises in the axil of a leaf on the stem. It consists of a short axis called a strig, occupying a central position and bearing a number of leaves. These leaves are of two kinds. One kind appears in pairs. These are the persistent stipules of a bract leaf, which is now suppressed. The original bract leaves were arranged alternately in two rows up the axis, hence these pairs or "stipular bracts" form two double rows (pairs alternate) up the axis. On the mid-line between the members of each pair of stipular bracts, and just above them, are four little stalks each bearing a bracteole which subtends one female flower. Thus there are alternately, up the strig, groupings of six leaves, each group consisting of two stipular bracts subtending four flower-bearing stalks, and on each stalk a bracteole.

It is the stipular bracts and bracteoles, called collectively the "petals," which are the valuable parts of this whole unit. They proceed to full development, no matter if the flowers are pollinated or not. If the flowers are pollinated the individual strobiles become heavier, due to a slight enlargement of the "petals" and the presence of developed fruits. Buyers usually pay rather less per pound for hops which have been pollinated, but such is the increase in the weight of crop harvested per acre that it may pay the grower best to include in his hop garden a few male plants to supply pollen and so produce "seedy hops."

Lupulin of Hops

The commercial hop is useful because the bracts and bracteoles bear on their surface peculiar secretory structures. The secretion is a complex mixture of essential oils and resins known as *lupulin.* Different varieties of hop plant produce different amounts of lupulin. The composition of the lupulin, too, varies among different varieties, and hence they are used for different purposes according to the character of the lupulin they produce. It is

on the total content of lupulin and the proportions of the various constituents in it that any particular consignment is valued.

The lupulin-containing hairs or glands occur scattered all over the "petals," but never on vegetative leaves outside the strobile. When ripe they are yellow-gold in colour, and to the unaided eye resemble pollen-grains. When magnified they are seen to be formed of a very short stalk bearing a cup-shaped structure of secretory cells. The secretion, lupulin, is produced by these cells into the inner aspect of the cup, which eventually becomes completely filled. Stretching from lip to lip of the cup so as to enclose and protect the lupulin is a thin membraneous skin.

When hops are ripe the long stems or bines of the plant are pulled off the supports up which they have twined and the inflorescences stripped off. These are dried and variously treated. In the brewing industry the lupulin of the hop is used to give a characteristic flavour to the beer, in which it also acts as an antiseptic.

Pineapple, Fig

Two other inflorescences which come into commerce as such may be noted in passing. One of these is the pineapple, valued for its succulent fruits massed compactly on a succulent central axis of the inflorescence. The other is the fig, which is composed mainly of a cup-shaped axis of inflorescence analagous to the cup-shaped torus of the rose hip. The pips of the fig, however, are not the product of the many free carpels of one flower as in the rose, but each pip is produced by a one-carpelled individual flower, many of which make up the inflorescence.

Grass Inflorescence

The flowering region of grasses is important to agricultural botanists, not only because it and the long culm on which it is borne adds considerably to the hay yield, but because of its ready use in the identification of the different kinds of grasses.

There are two main types of grass inflorescence. On the one hand there is the *panicle*, where a main axis bears branches on which the flowering units are borne. On the other hand there is the *spike* with an unbranched main axis, with the flowering units sessile on it.

FIG. 78

The Grass Inflorescence: the Panicle

(*a*) Simple—branches of the rachis not branched (sterile brome)

(*b*) Compound—branches of the rachis branched (wavy hair grass)

(*c*) Compound—secondary branches bearing spikelets massed in compact groups (cocksfoot)

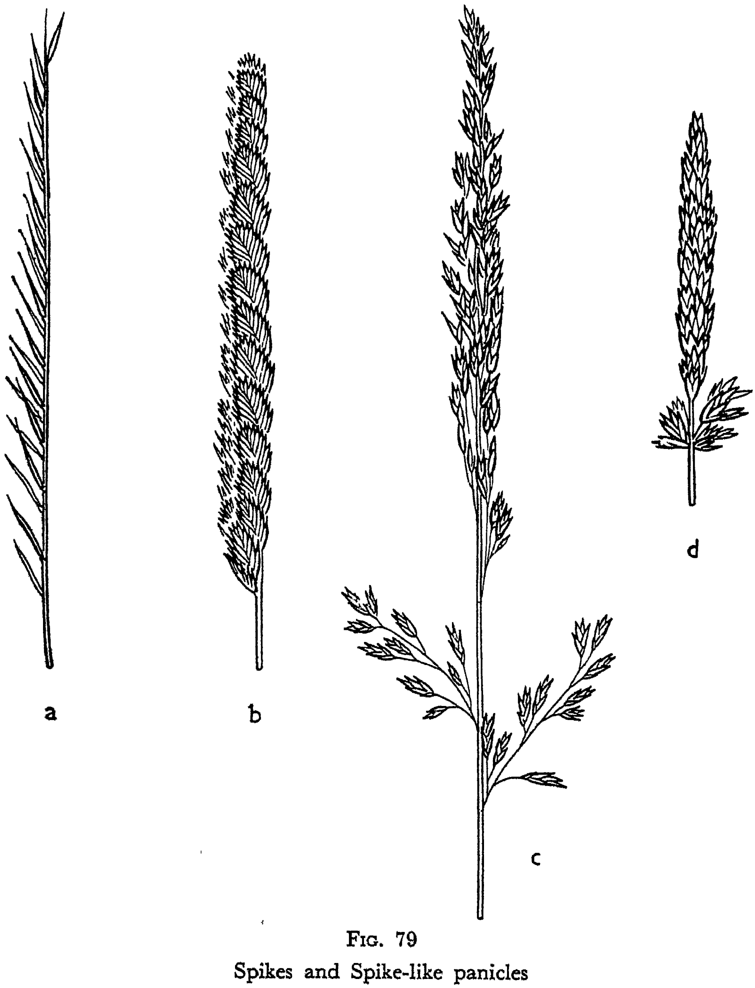


FIG. 79

Spikes and Spike-like panicles

(*a*) One-sided spike of Moor Mat-grass; (*b*) One-sided spike of Dogstail; (*c*) Loose spike-like panicle of Purple Molinia; (*d*) Loose spike-like panicle of Koeleria (in (*c*) and (*d*) the lowest branch is pulled out)

A somewhat intermediate form bears the flowering units on very short branches of the main axis. These units appear to be sessile, and the inflorescence simulates a spike. Such an inflorescence is called a spike-like panicle.

The main axis of any of these inflorescence types with lateral members inserted on it is likened to the backbone of a fish, or the mid-rib of a feather, and hence is named the *rachis*. In

the spike type the rachis is not branched ; in the panicle it is branched. If the primary branches of the panicle are themselves un-branched it is said to be simple ; if they are branched the head is referred to as compound panicle.

The variations in grass inflorescence are very useful in identification, and will be discussed in detail later. The arrangement of parts of the flowering units must first be outlined.

The Flowering Unit of Grasses : The Spikelet

Each unit consists of a short central axis called the *rachilla*, a diminutive of rachis. The rachilla, where it arises on the rachis or on one of its branches, is subtended by a pair of leaves called *glumes* ; one is basal and called the lower glume ; the other is a very little way up the rachilla on the opposite side, and is called the upper glume. These two leaves *subtending the unit as a whole* may be regarded as analagous to bracts. Above the glumes, arranged alternately in two rows up the rachilla, are a number of flowers. Each flower, individually, is subtended by a pair of leaves called *pales*. One of these is inserted at the base of the flower at the junction of the rachilla and the flower stalk ; it is called the lower pale. The other pale placed a little nearer the flower is called the upper pale.

The whole structure of glumes, rachilla, pales, and flowers is called a *spikelet* in recognition of its likeness to a diminutive spike. All grasses whether having a paniculate or spicate inflorescence bear their flowers in spikelets.

A grass spikelet, then, is a unit composed of one or more flowers. When more than one flower is present they are arranged alternately, in two rows on the short axis or rachilla. The whole is subtended by bract-like leaves or glumes, usually two in number. Each individual flower on the axis is subtended by bracteole-like leaves or pales, usually two per flower.

Types of Glume and Pale

The glumes and pales of the spikelet differ in shape, size, and occasionally in number in different grasses. These characteristics are used for purposes of identification.

Some pales and glumes have the mid-rib prominent, which gives the leaf the cross-section seen in a yacht ; these are described

FIG. 80

A seven-flowered Grass Spikelet

Left At base are two small glumes (lower and upper). Then the first flower with large lower pale and small upper pale. Flowers with similar L.P. and U.P. occur alternately in two rows up the rachilla

Right A single flower with its axis exaggerated. Lower pale, upper pale, two lodicules, three stamens, and gynæceum with two stigmas

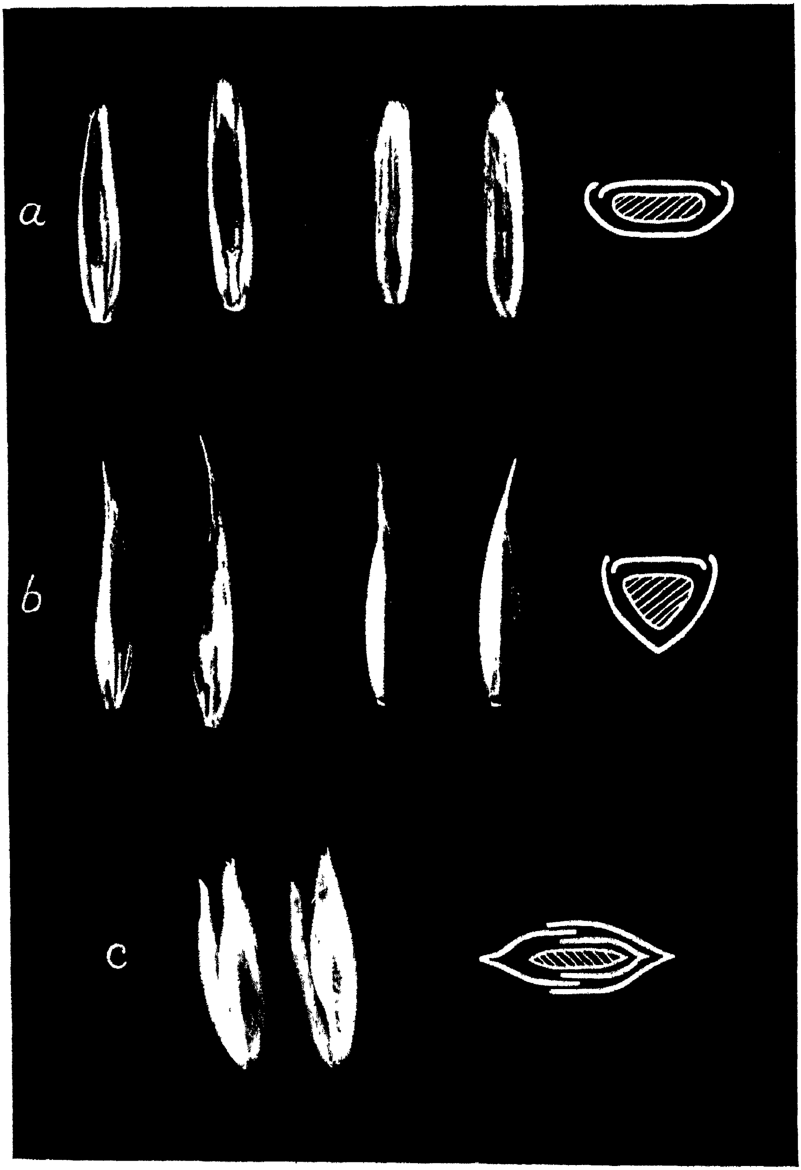
as keeled. In others, the shapes of the leaves resemble more a flat-bottomed punt; these are described as not-keeled or round. Some are membraneous or have membraneous margins. Some are hairy, others are free of hair. A feature easily observed is the presence or absence of an *awn*. This, when present, is seen as a bristle-like structure continuing the mid-rib on the pale or glume.

The position of the insertion of the awn is important. It may appear as a straight continuation of the mid-rib from the apex of the glume or pale which bears it. Such an awn is said to be terminal. It may spring from the mid-rib halfway up the back of the leaf, when it is said to be dorsal. An awn which arises at the base of the leaf is described as basal. Insertions of the awn intermediate between these are described as sub-terminal or sub-dorsal.

PLATE 43 THE GRASS FLOWER

The flower of Oat with pales removed. The three stamens are seen right, left, and behind the central body which is ovary. The ovary is superior. The two feathery styles/stigmas arise on the apex of the ovary

PLATE 44 GRASS "SEEDS"



(a) Round-backed or barge-like: Lies on a table face-up or back-up (Ryegrass)
(b) Keeled or yacht-like: Lies on side or back-up (Cocksfoot)
(c) Doubly keeled: Lies on side only (Yorkshire Fog and Foxtail)

Note the twist on the awn point of the lower pale of Cocksfoot

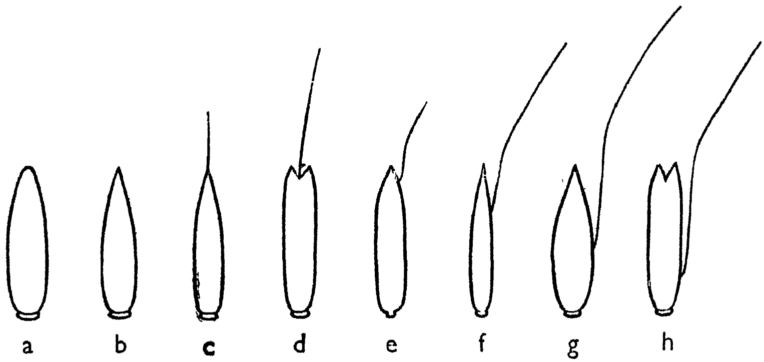


FIG. 81

Position of Awns

(*a*) awnless
(*b*) awn point
(*c*) terminal
(*d*) mucronate terminal
(*e*) subterminal
(*f*) subterminal or dorsal
(*g*) dorsal
(*h*) subdorsal

The Grass Flower: A Reduced Lily Type

The flowers of the grass spikelet may each be pictured as of a lily type in which there has been considerable reduction of parts. The simplest lily flower is represented by the floral formula, Ѵ Ca 3 Co 3 And 3 + 3 Gn ($\underline{3}$), and provides a floral diagram as seen in Fig. 82. The members of the two whorls of stamens are on alternate radii, the outer ones alternate with the petals.

The Perianth

In the grass flower sepals are never present, the duty of protecting the reproductive parts having been taken over by the glumes and pales. The petals too may be completely gone, or two of them, or all three may be present as small scales called *lodicules*. The duty of these much modified petals is not attraction of insects, for the grass flower is wind pollinated, but the pushing apart of the pales when the " flower " opens.

The Andrœcium

Different kinds of grass show different degrees of loss in the stamens. Bamboos and rices show six stamens in two whorls, just like the simple lily. Most cultivated grasses show only three in one whorl; it is believed that what would have been the inner whorl is gone. The loss of parts has gone still further in some.

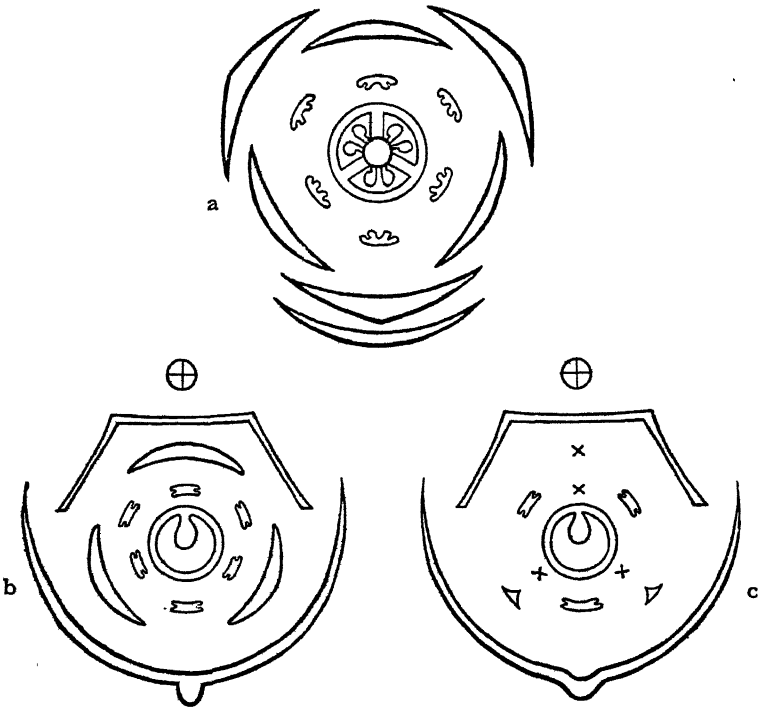


FIG. 82
Floral diagrams
(*a*) lily (compare with colour plate XII) ; (*b*) bamboo (pales = bracteoles shown) ; (*c*) typical grass (pales = bracteoles shown)

For example, sweet vernal grass has only two stamens, while rat's-tail fescue has only one.

The Gynæceum

The gynæceum in a grass consists of a one-chambered superior ovary with one ovule. There are usually two styles and stigmas. The presence of these suggests the presence of two carpels, but in practice it is probably best to regard the structure as monocarpellary.

Imperfect Flowers

In particular flowers of some grasses the gynæceum is absent, as in the lower flower of the spikelet of tall oatgrass or the upper

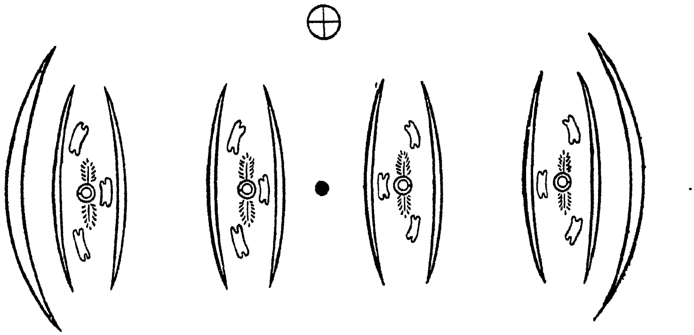


FIG. 83
Spikelet diagram of Couch Grass—edge-on type
(Note position of rachis)

flower of Yorkshire fog. Flowers with stamens only are said to be staminate, imperfect, or male. The floral formula of the "standard" grass may be written ⚥ $Ca_0\ Co_0\ And_3\ Gn_1$.

The Spikelet Diagram

The floral diagrams of grasses usually convey very little information. The diagram of the spikelet, on the other hand, may be of the greatest interest. In drawing these, particular attention should be paid to showing the position of the rachilla, and in the case of spike inflorescences of the rachis.

In order to realize this point the spike inflorescences of wheat and barley, or couch and ryegrass, should be compared. First of all, each member of one of these pairs should be held with

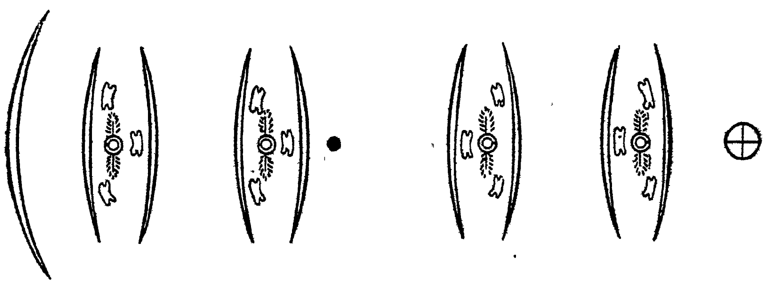
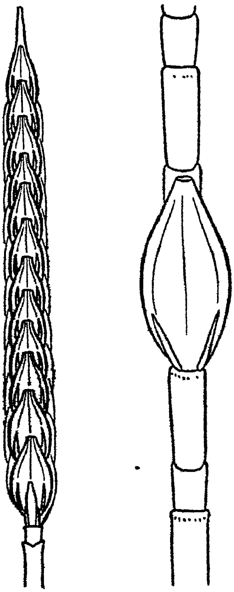
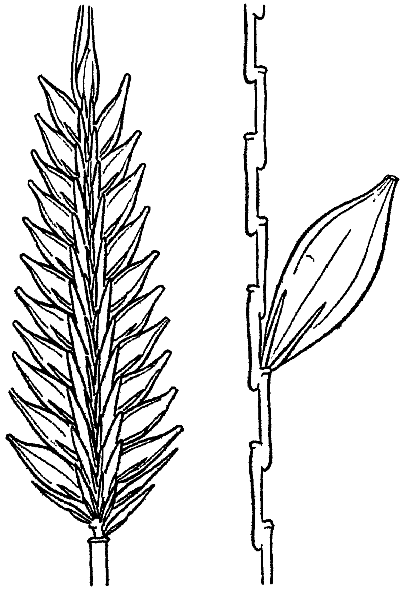


FIG. 84
Spikelet diagram of Ryegrass—back-on type
(Note position of rachis)
The upper glume is missing in this spikelet; protection is afforded by the rachis on this aspect

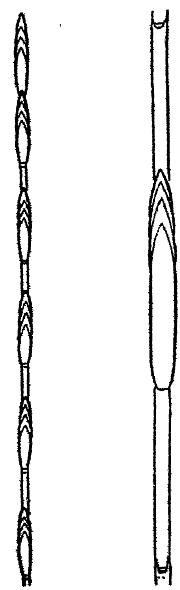
TWO-SIDED SPIKES BACK-ON TO RACHIS



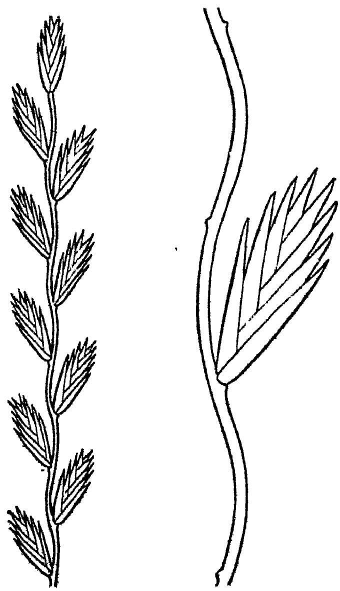
Barley, correct view



Barley, incorrect view



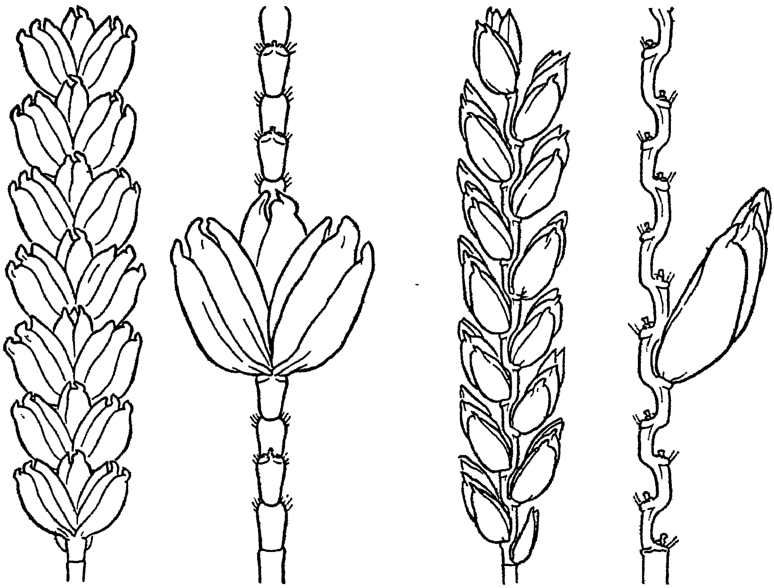
Ryegrass, correct view



Ryegrass, incorrect view

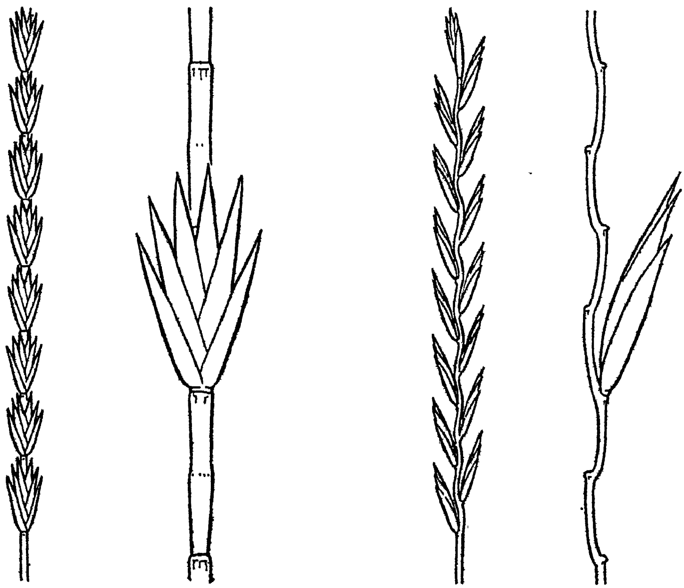
FIG. 85

TWO-SIDED SPIKES EDGE-ON TO RACHIS



Wheat, correct view

Wheat, incorrect view



Couch, correct view

Couch, incorrect view

FIG. 86

the rachis vertical in such a way that a line from the eye of the observer passes through the centre of a spikelet to the rachis. If this line reaches the rachis by any route other than through the *centre* of an individual spikelet, the culm should be turned on its own axis till the proper arrangement is reached. When this is done with barley (a two-rowed variety is simplest) or ryegrass the line passes through the mid-dorsal region of all the pales and glumes. The *back* of the upper glume is seen to touch or abut on the rachis. *The spikelet is set " back-on " to the rachis.*

When wheat or couch is treated similarly the line passes between the margins of the leaves of the spikelet. The *edges* of the glumes and pales touch or abut on the rachis. *The spikelet is set " edge-on " to the rachis.*

Features of the Grass Plant used in Identification

It will be useful now to see how variations in different features of the flowering region of grasses may be used in their identification. Tables V and VI (pp. 200–207) show all the characteristics of different grasses, arranged in such a way as to bring together, in groups, all the kinds having a salient feature in common.

The differentiation of grasses into those with spikes, spike-like panicles, and panicles is simple.

Floristic Features of Grasses with Spike Inflorescences

Amongst those with spike inflorescences there are some in which the spikelets are arranged in only one row to give a one-sided spike, as is seen in moor mat-grass and dogstail. In others such as the ryegrasses, couch grass, and wheat the spikelets are alternate in two rows. The members of these two sub-groups are subdivided according to the number of spikelets, which occur at each level of the rachis. In moor mat-grass, ryegrass, couch, and

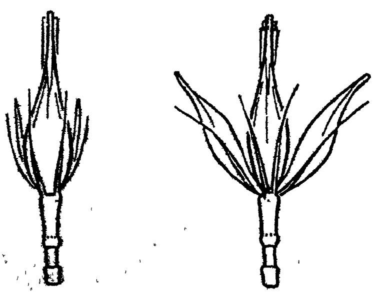


Fig. 87

Barley Spike

Left A two-rowed variety

Right A six-rowed variety

Only one node of the rachis is shown in each case. (In the two-rowed form the lateral spikelets are represented by bristle-like glumes and pales.)

wheats the spikelets appear solitary, while in dogstail there is a cluster of spikelets at each level.

In the barley spike a group of three spikelets appears at each point up the rachis. They appear to be arranged in groups of three with the groups alternate. The whole inflorescence looks as if the rachis has six rows of spikelets running up and down it. A more accurate interpretation is that at each notch of the rachis a small branch arises. This carries one spikelet terminal and two lateral. These three-spikeleted branches are alternate up the rachis. On a strict interpretation the inflorescence of barley is really a spike-like panicle.

In some barley varieties only the flower of the terminal spikelet of each trio is fertile ; the flower of each lateral is staminate. When ripe the fat, fruitful, terminal spikelets are in two distinct rows up the axis, and the laterals appear as thin, almost bristle-like structures.

In other barleys all three spikelets of each trio are fertile, and all three form fruits, hence the mature, plump spikelets are in three rows up each side of the rachis. These are the six-rowed barleys. If the maturing grains of such an inflorescence develop well the enlarging spikelets are constrained for room round the central axis. The laterals at or about the same level jostle each other, and eventually the lateral of one branch slips in above the lateral of the other. This occurs on the two opposite sides of the rachis, and the spikelets appear arranged in four rows. Varieties with this characteristic are called the four-rowed barleys.

The final stage in identification by floristic features is reached on the basis of individual idiosyncrasies. For example, the cluster of spikelets in dogstail consists of a perfectly normal spikelet " subtended " by a spikelet with several imperfect and sterile flowers. The ryegrasses, with the " back " of each spikelet sunk into a longitudinal furrow of the rachis, has no need of an upper glume for protection on that side. In these grasses this leaf is suppressed in all spikelets except the one which occupies the terminal position on the rachis, which is exposed on all sides.

Floristic Features of Grasses with Spike-like Panicles

Amongst the spike-like panicles, those of timothy and the fox-tails simulate a spike most. The branches are so short and set so closely on the rachis that it is only when the units are pulled

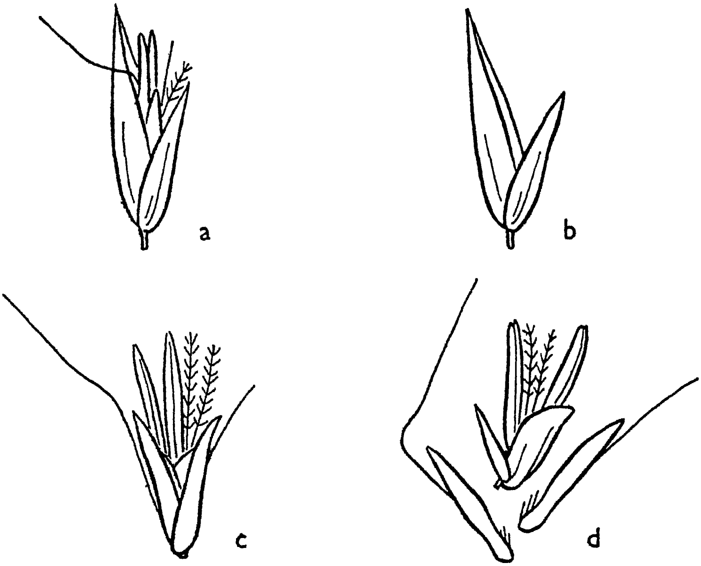


FIG. 88

Dissection of spikelet of Sweet Vernal

(*a*) The entire spikelet; (*b*) the outer glumes; (*c*) the spikelet—outer pair of glumes removed; (*d*) the pales and flower exposed by removal of inner pair of glumes

apart that the paniculate nature of the inflorescence can be seen. The spikelet details of the different grasses with spike-like panicles yield excellent data for differentiation. Timothy, sweet vernal, marram, and the foxtails, grasses of this group, all have only one flower per spikelet. Of these the foxtails only lack an upper pale. Only sweet vernal has two pairs of glumes arranged alternately. These are described as a lower outer glume, an upper outer glume, a lower inner glume, and finally, an upper inner glume. Timothy has one pair each of pales and glumes. Marram grass is a much bigger, coarser grass, and there is a tuft of hairs at the base of each lower pale. Other features, of the awns, shape of spikelet, and so on are equally clear cut.

PANICULATE GRASSES

Amongst the more numerous paniculate grasses differentiation may be a little more difficult. Cocksfoot and one or two other grasses may be recognized by the spikelets being massed in groups or tufts at the ends of the branches of the rachis. In

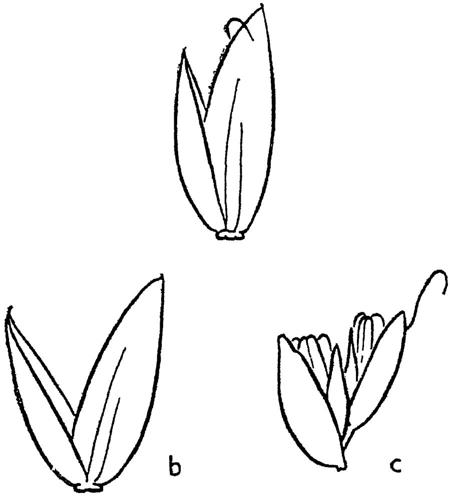


FIG. 89

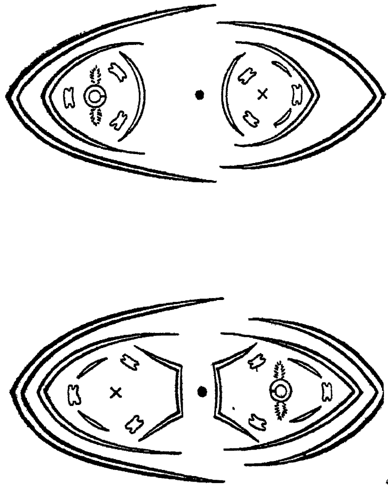
Dissection of spikelet of Yorkshire Fog

(*a*) The entire spikelet; (*b*) the glumes; (*c*) the glumes removed to expose the lower, hermaphrodite flower and the upper, male flower. In each of these the pales are apart and expose the flower parts

(Note the " fish hook " awn subterminal on the lower pale of thè upper flower)

others, where the spikelets are more evenly distributed, the branches though distinct may be short and not spreading, so that the inflorescence comes near to the spike-like condition. This is seen in false brome-grass, purple molinia, and sheep's fescue. Other grasses with normally branched panicles may show the typical open condition only while the flowers are actually distributing and receiving pollen. For example, in Yorkshire fog, the branches of the rachis alter the angle they make with the main rachis so that the spikelets are massed up together about the rachis before and after flower opening, but are all separate in space while pollination is active.

Characters of the spikelet and individual leaves are referred to more in the paniculate grasses than in the spicate and spike-like forms. The number of flowers per spikelet now becomes a major character. Some, such as Agrostis (bent-grasses), have only one. Tall oatgrass and Yorkshire fog both have two flowers per spikelet, but in the oatgrass the lower one is staminate, while



ERRATUM—page 196, Fig 90

Amended title

Diagram of two-flowered mixed spikelets

Above Yorkshire Fog with upper flower unisexual (male)

Below Tall Oatgrass with lower flower unisexual (male)

in Yorkshire fog the upper is without gynæceum. The awns, too, differ in these grasses. In the oatgrass the lower pale of the lower flower bears in the dorsal position a long awn. This is sharply bent like a knee at its mid-point, and it is said to be kneed. The fog grass has a small awn resembling a fish-hook in the sub-terminal position of the lower pale of the upper flower. Paniculate grasses with two or more perfect (hermaphrodite) flowers per spikelet comprise the bromes, fescues, the meadow-grasses, and many others. The fescues have a terminal awn on the lower pales, while all the bromes, except upright brome, are charac-

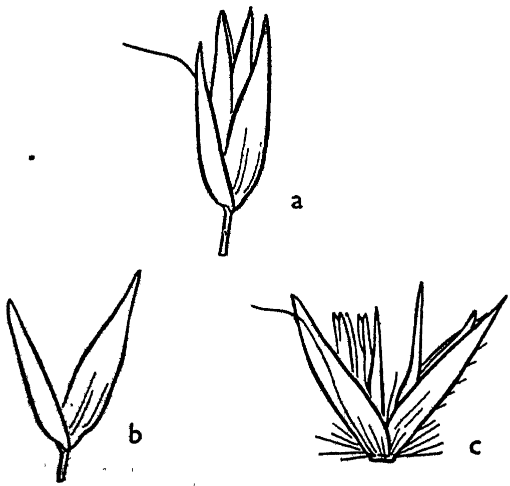


FIG. 91

Dissection of Tall Oatgrass spikelet

(*a*) Entire spikelet

(*b*) The glumes

(*c*) The two flowers with their pales

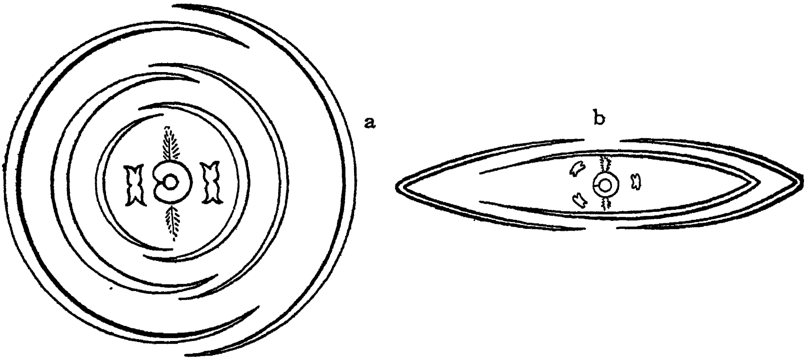


FIG. 92

Spikelet diagrams

(*a*) Sweet vernal grass. Note there are two pairs of glumes and the stamens are reduced to two. (*b*) Foxtail. The upper pale is missing in this one-flowered, doubly keeled spikelet

terised by having on each lower pale a sub-terminal awn, which arises very much as the mucronate point does on a medick leaflet. The meadow-grasses never have any awn in the spikelet.

The various characters which may be of use in identification of a grass inflorescence are included in Tables V and VI.

POLLINATION AND FERTILIZATION OF GRASSES

The pollen of many grasses blows free on the wind, and when drawn into the nose of a human being may cause hay fever. The pollen is collected by pharmacists, and from it a preparation is made which is used to immunize those people who are allergic to the spores.

The opening of the grass spikelet for release and receipt of pollen is due to the lodicules which swell up. The pales are caused to turn as on a hinge at their point of attachment and so swing apart. At the same time the thin, delicate filaments of the stamens and the styles elongate so that they come to hang free, well outside the spikelet. The filament of the stamen is attached to the mid-dorsal position of the anther which dehisces at its ends. The light pollen is slowly sprinkled out as the anthers sway in the breeze. The stigmas are like little feathery brushes, specially suited to catch the air-borne pollen.

Some grass spikelets do not open because lodicules are absent, the pales do not swing apart, and the stamens and stigmas remain

inside. Self-pollination is almost invariable in these cases. Other grasses having no lodicules cannot part the pales, but the stamens and stigmas by the force of their growth push out between them and appear at the tips of the pales.

The Grass "Seed"—Simple Types

The result of successful pollination is that the ovary develops into a one-seeded fruit, the grain or caryopsis. The true seed is possessed of a bulky endosperm, usually of a starchy character. In order to get one-seeded parts for dispersal, a number of modifications have developed. In the simplest case, as in wheat, the grain itself separates, falls free, and the pales and glumes form the chaff. In others, the caryopsis remains invested in its pales, but the spikelet breaks up. The rachilla splits transversely at the base of each spikelet. The "seed" in this case consists of the grain fruit invested in a pair of pales and with a small piece of rachilla running from the base some way up the back of the upper pale. The oat is an excellent example of this type though naked oat is similar to wheat.

The Grass "Seed"—More Complex Types

In other more complex types, the seed consists of more of the spikelet parts. For example, in Yorkshire fog two kinds of seed are common. In one, the "shelled seed," each consists of the caryopsis produced by the lower fertile flower invested with its pales. This is equivalent to the simple case seen in oats. The other kind of Yorkshire fog "seed" consists of the entire spikelet with a caryopsis and attendant pales from the lower flower, a pair of empty pales and awn from the upper male flower, all invested in the keeled glumes still attached to the rachilla.

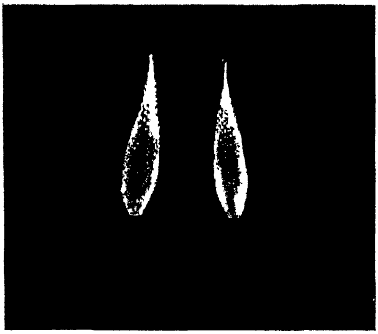
There is also "shelled" and "unshelled" "seed" of sweet vernal grass. The shelled "seed" in this case is a caryopsis invested in a pair of shiny, mahogany-coloured pales. The unshelled "seed" is the same but still invested in the inner pair of awned glumes.

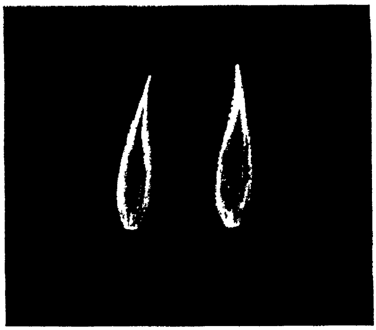
The features of the grass seed commonly used in identification are included in Table VII (pp. 208-211).

Anyone wishing to consult specialist literature on the grass flower or seed and their attendant parts may find the terminology

Smooth-stalked Meadow-Grass

Annual Meadow-Grass





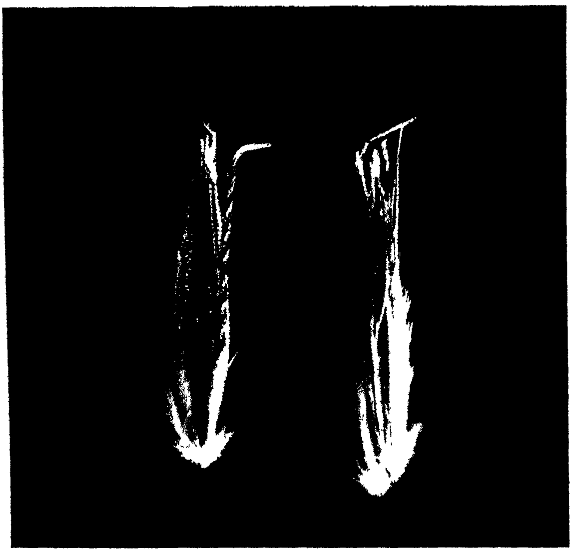
Two views of Dog's-tail. This seed has a twisted awn point but is round-backed (compare Cocksfoot, see Plate 44)

Shelled seed of Yorkshire Fog

(*Note:* The web of silky hair seen on Smooth-stalked Meadow-Grass is removed in machining commercial seed)

Meadow Foxtail. A one-flowered spikelet : U.P. missing ; subdorsal awn on L.P.

Golden Oatgrass. L.P. with bifid apex and awn sub-terminal



Tall Oatgrass. Two-flowered spikelet, lower one staminate ; awn twisted and kneed

PLATE GERMINATION TEST

Water is supplied from the tank to the seeds on the blotting-paper pads by the paper wicks. The glass bells prevent excessive evaporation. The tank is heated by an electric element (*Photo : Sutton and Sons Ltd.*)

PLATE 48 GERMINATION TEST

Hard seeds and normal seedlings as they appear on a test pad
(*Photo : Messrs. Sutton and Sons Ltd.*)

TABLES V, VI, VII

TABLE V.—SUMMARY OF THE FLORISTIC

I.—THOSE GRASSES IN WHICH THE INFLORESCENCE IS A SPIKE, THE BRANCHES

	Name	Form of Inflorescence and Arrangement of Spikelets	No. of Flowers in Spikelet	No. and Character of the Glumes
1	Moor Mat-Grass	one-sided spike ; spikelets solitary, back-on	1	none, or rudimentary L.G. present
2	Dog's-tail	one-sided spike ; spikelets clustered	3–5	2 equal, narrow, pointed
3	Perennial Ryegrass	two-sided spike ; spikelets solitary and back-on to rachis	6–10	U.G. absent ; L.G. long, narrow
4	Italian Ryegrass	ditto	6–10	U.G. absent ; L.G. long, narrow
5	Darnel or Drake	ditto	4–5	U.G. absent ; L.G. broad
6	Couch Grass	two-sided spike ; spikelets solitary, edge-on to rachis	4–5	2 equal ; long, narrow, sometimes hairy
7	Sea Lyme Grass	two-sided spike ; spikelets in pairs	3–4	2 nearly equal, long, narrow ; acute apices, woolly hair
8	Wall Barley	two-sided spike ; spikelets in trios	1	2 equal on each spikelet ; middle spikelet linear, fringed with hair ; lateral spikelets bristle
9	Meadow Barley	ditto	1	all bristle-like
10	Finger-Grass, or Bermuda Grass	Digitate group of 3 to 6 one-sided spikes ; spikelets solitary, edge-on	1	2 equal, narrow, keeled ; apices acute ; purple colour ; hair on keel.
11	Floating Sweet-Grass	very lax, simple panicle	6–∞	2 ; U.G. much longer than L.G. ; membraneous
12	Marram Grass or Sea Mat-Grass	panicle branches short, almost a spike ; spikelets all round rachis	1	2 narrow, boat-shaped; apices acute
13	Timothy or Herd's Grass	panicle branches short, almost a spike ; spikelets close packed all round rachis	1	2 equal ; broad, both keeled ; harsh hair all over ; fringe on keel

SPIKE-LIKE PANICLE, OR A PANICLE WHICH FROM THE POSTURE OF APPEARS SPIKE-LIKE

No. and Character of the PALES	AWNS	NOTES	
2, both linear ; L.P. longer, with scabrid keel and blue colour at base	terminal on L.P.	spikelets back-on in longitudinal depressions of the rachis	1
2, both linear ; L.P. longer, spotted and scabrid on upper third	awn-point on L.P.	each fertile spikelet " subtended " by an infertile spikelet of bristle-like glumes and pales	2
2 equal linear, apices rounded; L.P. boat-shaped ; no hair	none	glumes not as long as spikelet ; each spikelet in a longitudinal depression of the rachis	3
2 equal ; L.P. boat-shaped ; no hair	terminal on L.P.	ditto	4
2 equal ; L.P. broad and boat-shaped	terminal on L.P.	glumes as long or longer than spikelet; spikelets broader than Italian or Perennial	5
2 L.P. longer, boat-shaped, slight keel, hair all over ; U.P. hair on margin	glumes and L.P. have awn points	numerous closely related forms are known ; some hybridize with some wheats	6
2 nearly equal ; L.P. boat-shaped ; covered velvety hair	short point on L.P.	U.P. bifid at apex	7
2 equal on all spikelets ; those of mid spikelet boat-shaped ; others bristle	central spikelet ; glumes and L.P. terminal; laterals L.P. terminal	the flower of central spikelet only is fertile	8
2 equal	terminal on L.P.	ditto	9
hair on dorsal nerve and margins	none	the spikes arise at one level on top of culm, and are nearly erect	10
2 nearly equal ; hairless	none	allied to meadow-grasses ; grows usually in wet places	11
2 ; L.P. longer, with mid-rib toothed, and tuft of hair at base	awn-point or short awn on L.P.	a sand-binding grass of the seashore ; silky hair on the slender rachilla	12
2 ; L.P. larger, globular, silvery membraneous ; U.P. smaller linear	rough terminal on both glumes	the inflorescence quite spike-like, harsh to the touch ; many forms differing in form and cytologically	13

	Name	Form of Inflorescence and Arrangement of Spikelets	No. of Flowers in Spikelet	No. and Character of the Glumes
14	Meadow Foxtail	panicle branches short, almost a spike; spikelets close packed all round rachis	1	2 equal; broad, both keeled; apices acute; soft hair all over
15	Slender Foxtail	ditto	1	as above, but keels only slightly hairy
16	Floating Foxtail	ditto	1	2 equal; both keeled; apices blunt; keels fringed hair
17	Canary Grass	egg-shaped, spike-like panicle; spikelets close packed all round rachis	1	2 pairs; inner small, narrow, boat-shaped; outer large, keeled; winged membrane on keel
18	Wood False Brome	panicle branches short, erect, and close to rachis; spikelets terminal on branches	7–15	2 equal; broadest at base; hairy
19	Heath False Brome or Tor Grass	ditto	8–12	U.G. twice length of L.G.; mid- and inter-veins well developed
20	Sweet Vernal Grass	panicle, 2–3 short, erect branches at each "node"; spikelets terminal	1	2 pairs, outer; linear, acute, sparse, yellow hair, inner; equal, keeled; dense brown hair
21	Heath Grass	simple panicle; spikelets terminal	3–4	2; L.G. longer than U.G.; both rounded, hairless membraneous
22	Crested Hair Grass	compound panicle; branches short and erect; spikelets in tufts at tips of branches	2	2 equal length; L.G. narrow; U.G. broader; both keeled, hairy
23	Purple Molinia	compound panicle; several primary branches at each "node"; spikelets diffuse	2-4	2 equal, linear, pointed, hairless; pink to purple colour mostly at margin
24	Sheep's Fescue	compact, one-sided compound panicle; spikelets diffuse	4–6	2; L.G. shorter than U.G., hairless
25	Rat's-tail Fescue	compact, one-sided compound panicle; primary branches long, secondaries short	5–6	2; L.G. slightly longer than U.G.; both linear; U.G. 3-nerved

continued

No. and Character of the PALES	AWNS	NOTES	
U.P. missing ; L.P. keeled	sub-dorsal on L.P.	the inflorescence quite spike-like (see Plate 43) ; soft to the touch ; flowering early in spring	14
ditto	ditto	inflorescence rather harsh to the touch	15
ditto	ditto	inflorescence about 1 inch long, and very slender ; spike-like	16
2 equal ; apices acute ; hairy when young, shining when ripe	none	inflorescence light green when young ; paper white when ripe	17
2 ; U.P. shorter than L.P. ; U.P. rounded apex ; hair on veins	short on both glumes, long terminal on L.P.	each spikelet as long as the distance between insertion of two branches ; rachilla hairy	18
2 ; L.P. rather longer with hair on margins ; U.P. apex square cut	short terminal on L.P.	ditto	19
2 equal, keeled, smooth, shining	inner glumes ; straight dorsal on lower ; kneed ; twisted dorsal on upper	flowers with two stamens only, flowering early in spring. Puel's S. Vernal has yellow inner glumes, and is an annual	20
2 ; L.P. larger than U.P., membraneous, inflated	none	few (2–6) spikelets per head	21
2 ; L.P. rather longer ; U.P. folded in on flower, and margins fringed	none	flattened spikelets in tufts resembles cocksfoot, but branches of the rachis short	22
2 equal ; L.P. linear, keeled, pointed, pink especially at margin ; U.P. narrow, colourless	none	rachilla of each flower is kneed when ripe, and terminates in a disc fringed with hairs	23
2 ; L.P. boat-shaped, hairless	awn point on L.P.	there are many forms of this grass, mostly perennial	24
2 equal, linear, rough	long, terminal on L.P.	each flower has one stamen only, and the plant is an annual	25

TABLE VI.—SUMMARY OF THE FLORISTIC

II THOSE GRASSES IN WHICH THE

	Name	No. of Flowers in Spikelet	No. and Character of the Glumes
1	Brown Bent or Velvet Bent-Grass	1	2 unequal; acute keel on L.G. saw-toothed
2	Brown-top, Colonial Bent or Rhode Island Bent-Grass	1	2 almost equal; acute apices; keel of L.G. saw-toothed on upper half only
3	Silky Bent Grass	1	2; L.G. longer than U.G.; both linear; L.G. saw-toothed on upper half of keel
4	Reed Canary Grass	1	2 equal, both keeled, apices acute, and surfaces smooth
5	Yorkshire Fog	2	2 nearly equal in length; U.G. broader; both compressed, keeled and hairy all over
6	Creeping Soft-Grass	2	differs from above; in G.s more acute apex, not so hairy, keels toothed, U.G. narrower
7	Tall Oat-Grass	2	2; both with short hairs; U.G. larger, with one nerve; L.G. smaller, with three nerves
8	Wavy Hair-Grass	2	2; L.G. shorter, both keeled, acute apices; membraneous, white and shining
9	Tufted Hair-Grass, Tussock Grass	2	2, both keeled; L.G. shorter and narrower, apex bifid, lower dorsal region purple-red; U.G. longer with acute apex
10	Golden Oat Grass	2 to 3	2; both narrow; keeled with acute apices pale yellow, membraneous
11	Wild Oat Grass	2 to 3	2 nearly equal; slight keel; thinly membraneous, inter-nerves well marked

CHARACTERS OF SOME COMMON GRASSES

INFLORESCENCE IS A TYPICAL PANICLE

No. and Character of the Pales	Awns	Notes	
1 ; U.P. absent or rudimentary ; L.P. 3 times longer than broad ; smooth, glossy	fine ; dorsal on L.P.	the bent grasses all have light, graceful, open compound panicles ; branches at flowering distributed all round rachis ; all have one-flowered tiny spikelets ; the different characters vary considerably between different forms ; the three members shown here are fairly typical	
2 ; L.P. 3 times longer than broad ; margins overlap ; margins of U.P. basal tuft of hair	none		
2 ; L.P. boat-shaped tuft of hair on base	very long ; sub-terminal on L.P.		
2 equal, boat-shaped ; L.P. glossy, hair on margin ; U.P. upper margin fringed hair	none	two lateral tufts of hair at base of L.P. ; the culm 3–6 ft. high ; panicle plume-like ; plant usually on wet land or in water	
L.P. (both flowers) larger and deeply keeled ; shining	short, terminal on L.G. ; "fish-hook" sub-terminal on L.P. of upper flower	the LOWER flower BISEXUAL, upper flower male only ; the male flower is smaller ; the awn difference is diagnostic ; the inflorescence is spreading only at flowering time	
ditto	kneed on L.P. of upper flower		
2 equal, boat-shaped ; apices ragged ; margins fringed hair	long, kneed sub-dorsal on L.P. lower flower, and sometimes sub-terminal on L.P. upper flower	the UPPER flower BISEXUAL, lower flower male only ; the awn is straight in young flowers, and becomes twisted and kneed at maturity	
2 equal length ; apices acute, split, and ragged ; L.P. broad ; U.P. linear ; hair only on base of rachilla	kneed ; twisted basal on L.P.	the culm, rachis, and branches fine and wire-like ; the plant is smaller than its relative next below, but spikelets are larger	
2 equal ; L.P. boat-shaped ; long hairs on rachilla and base of L.P.	twisted and slight kneed basal on L.P.	large graceful inflorescence, culm 2½ to 4 feet high ; whole plant very rough ; habitat wet, sour land	
2 ; L.P. longer and broader ; both ragged at apex ; basal tuft of hair on L.P. ; hair on rachilla	twisted and kneed sub-terminal on L.P.	branches erect, parallel with rachis, except at flowering ; inflorescence golden yellow when ripe	10
2 nearly equal, acute apices ; colour, straw to dark brown	twisted and kneed dorsal on L.P.	related to cultivated oat, and this, the "Fatua" type, often appears in the crop	11

	Name	No. of Flowers in Spikelet	No. and Character of the Glumes
12	Perennial Oat-Grass	3 to 5	2; U.G. longer than L.G. pointed and keeled; upper margins of U.G. membraneous
13	Common Reed Grass	3	2; narrow, acute keel; intermediate nerves well marked
14	Cocksfoot or Orchard Grass	3 to 4	2; L.G. longer, acute keel, saw-toothed; U.G. membraneous
15	Rough-stalked Meadow-Grass	2 to 4	2; U.G. larger; both keeled, saw-edge on keel
16	Smooth-stalked Meadow-Grass or Kentucky Blue Grass	2 to 5	2; U.G. larger; both keeled; top third of keel of L.G. toothed
17	Wood Meadow-Grass	2 to 5	2 almost equal; L.G. 3-nerved, with slight keel
18	Annual Meadow-Grass	3 to 5	2; L.G. shorter and broader and keeled; both with membraneous margins
19	Flat-stemmed Meadow-Grass or Canada Bluegrass	4 to 6	2; almost equal, keeled, purple colour
20	Reed Sweet Grass	5 to 10	2; almost equal length; apices blunt; L.G. narrower, keeled, with no intermediate nerves
21	Meadow Fescue	5 to 10	2; L.G. shorter, narrower, more acute at apex; both membraneous in upper region
22	Field Brome Grass	7 to 10	2; L.G. smaller, with 3 nerves; U.G. larger, with 7 nerves; both smooth; membraneous margins
23	Sterile Brome Grass	5 to 10	2; L.G. shorter, narrower, almost bristle. U.G. larger, membraneous, mid-rib well defined and scabrid (no intermediate veins)
24	Upright Brome Grass	4 to 8	2 about equal, long, narrow; mid-rib saw-toothed

continued

No. and Character of the Pales	Awns	Notes	
2 equal, long, narrow, boat-shaped ; L.P. membraneous at margins and apex U.P. ; all membraneous	twisted and kneed sub-terminal to dorsal on L.P.	inflorescence simple and resembles spike ; rachilla hairy	12
2 ; L.P. long, narrow, twice length of U.P. ; its upper margin fringed hair	none	inflorescence first silvery violet, later chocolate ; rachilla bears long silky hairs ; culm 5–8 ft. high ; habitat aquatic	13
2 ; L.P. keeled, longer than U.P. by extent of awn point	awn point twisted on L.P.	spikelets in dense tufts at end of spreading branches ; a very valuable top-grass	14
2 about equal, L.P. keeled, web on base	none	topmost leaf of culm with long, pointed ligule ; culm between this leaf and first branch of inflorescence rough	15
2 ; L.P. slightly longer, keeled, rounded apex, dense web at base	none	ligule topmost leaf of culm ; short and blunt ; culm below inflorescence smooth	16
2 ; L.P. longer, keeled, acute apex ; hair on margin and lower half of keel ; thin web	none	inflorescence light and delicate ; nodes on culm, narrow bands, deep violet colour	17
2 ; L.P. rotund on lower half ; narrow and tubular on upper half ; soft hair all over ; no web	none	culm about 1 ft. high ; flowers all year ; very common	18
2 equal ; L.P. keeled ; hair on lower half of keel and nerves ; web	none	the tillers very flat, due to extreme folding of leaves in the bud	19
2, almost equal length ; L.P. broader, rounded at apex, veins prominent	none	culm tall ; panicle spreading ; aquatic or semi-aquatic habitat	20
2 equal length ; both round apex ; L.P. boat-shaped	none	a close relative ; tall fescue is larger, coarser, and L.P. has awn point	21
2 ; L.P. flat, boat-shaped, upper margins membraneous and fringed hair ; U.P. narrow membraneous strap	mucronate on L.P.	rachilla bears hairs ; a large number of forms are known ; all bromes except upright brome have awn mucronate on L.P.	22
2, both long, narrow ; L.P. margin overlaps margin of U.P. ; distinct nerves	mucronate on L.P. long	inflorescence graceful and drooping ; spikelets harshly downwards rough	23
2 ; L.P. longer ; pointed apex, rough, hairy, distinct veins	terminal on L.P.	rachilla hairy	24

TABLE VII.—SUMMARY OF FEATURES USEFUL IN THE RECOGNITION OF SOME COMMON GRASS SEEDS

Small = $<$ 5 mm. ; medium = $>$ 5 mm. and $<$ 7 mm. ; large = $>$ 7 mm. (length exclusive of awn when present)

NO AWN

Small Seeds, Keeled	
Annual Meadow Grass	Hair on nerves of L.P. No web ; body of seed somewhat globose on lower half, tapering on upper half
Canada Blue Grass	Hair on lower half of nerves of L.P. and margins of U.P. ; delicate web
Wood Meadow Grass	Hair on lower half of keel and margins of L.P. Apex of L.P. pointed. Web present
Smooth Stalked Meadow Grass	Hair on lower half of keel and margins of L.P. Apex of L.P. blunt and ragged. Web present
Rough Stalked Meadow Grass	Hair on lower half of keel of L.P. Apex of L.P. acute and keeled, not ragged. Web present
Shelled Yorkshire Fog	Few fine hairs at base of L.P. Side view of seed oval. L.P. smooth, whitely transparent
Shelled Sweet Vernal	No hair. Side view of seed sharply pointed. L.P. brown ; not transparent
Small Seeds, Round Back	
Timothy (Herd's) Grass	No hair ; seed globose ; pales silvery white
Quaking Grass	No hair. L.P. inflated with membraneous margins ; seed nearly as broad as long
Bent Grasses	Basal tuft of hair ; seed very small
Meadow Sweet Grass	No hair. Apex of L.P. rounded off ; dorsal nerve toothed ; seed size often M
Canary Grass	No hair when ripe. Apex acute ; L.P. glossy golden
Reed Canary Grass	Two lateral tufts at base of L.P. Apex not acute ; L.P. glossy
Large Seed, Round Back	
Perennial Ryegrass	No hair. Rachilla 4-angled in T.S. Sides straight and not parallel
Meadow Fescue	No hair. Rachilla cylindrical ; sides parallel and terminates in a knob
Awnless Brome Grass	Hair on rachilla, the nerves of L.P. and margin of U.P.
(The two last	members of this group may show a slight awn point)

AWN POINT

Small Seed Keeled	
Purple Molinia	No hair. L.P. and U.P. stand apart—side view of seed shows bifurcate apex. Rachilla kneed and terminates in a knob; seed nearly medium size
Small Seed, Round Back	
Sheep's Fescue (large sense)	No hair. Awn point not twisted or scabrid
Dogstail	No hair. L.P. twists on itself to form awn point, which is scabrid; seeds yellow to chocolate
Medium, Keeled	
Cocksfoot	Stiff hairs or scabrid teeth on upper part of L.P. keel. L.P. twists to run into awn point
Large, Round Back	
Tall Fescue	No hair. Seed similar to M. Fescue except for awn point
Couch Grass	No hair. Rachilla stout, concave at top
Sea Lyme Grass	Hair all over L.P., rachilla and margins of U.P.
Common Reedgrass	Hair on margins of U.P. and rachilla. L.P. twice as long as U.P.

TERMINAL AWN

Medium, Round Back	
Wall Barley Grass	Hair on margins of glumes. Seed consists of a central fertile spikelet and of lateral sterile spikelets
Rat's-Tail Fescue (Hair Grass)	No hair. Seed very slender and L.P. tapers gradually into a very long awn
Large, Round Back	
Moor Mat Grass	No hair. L.P. twists into long awn point or terminal awn. Prominent mid nerve may suggest keeled
Italian Ryegrass	No hair. Sides of rachilla curved. Awn sometimes missing when apex L.P. is ragged
Wood False Brome	Hair on rachilla and margins of U.P. Awn long and serrate. Rachilla concave at apex

LARGE, KEELED	
Erect Brome	Hair on L.P. and rachilla; seed long and narrow. U.P. acute apex. Keel due to prominance of mid nerve of L.P.
Schrader's Brome	Hair on margins of U.P. Seed very large. Awn short, keel scabrid

SUB-TERMINAL AWN

SMALL, ROUND BACK	
Silky Bent Grass	Hair a basal tuft. Awn four times as long as seed
MEDIUM, KEELED	
Yorkshire Fog (not shelled)	Hair all over. Seed, two sharply keeled glumes enclosing two florets. Upper floret's L.P. carries awn, shaped when ripe like a fish hook
LARGE, ROUND BACK	
Field (Soft) Brome	Sparse hair on L.P. Seed broad and open. Apex of L.P. bifid with awn rising from base of notch
Darnel (Drake)	No hair. L.P. flatly bifid
LARGE, KEELED	
Marram (Sea Mat) Grass	Hair on margins of U.P. Awn very short and recurved

DORSAL AWN

SMALL, ROUND BACK	
Velvet Bent	Hair a basal tuft. Inner pale absent or reduced. A very small seed
SMALL, KEELED	
Sweet Vernal Grass (not shelled)	Hair, dark brown, on glumes. Seed consists of inner pair of glumes and one caryopsis enclosed in pales. Straight awn on L.G.; twisted and kneed awn on U.G.

MEDIUM, KEELED	
Golden Oat Grass	Hair on rachilla and a basal tuft. L.P. bifid. Awn twisted and kneed. Long narrow seed
Meadow Foxtail	Hair, soft, on keel. Seed = spikelet + L.G., L.P., U.P. (no U.G.). Awn on L.P. projects beyond glumes
LARGE, ROUND BACK	
Wild Oat Grass	Hair on lower half of L.P. and on rachilla, basal tuft. Awn long, twisted and kneed. Occurs often in crops of cultivated oats
Perennial Oat Grass	Hair, basal tuft and on rachilla. Awn twisted and kneed
Tall Oat Grass	Hair at base and on rachilla. Seed consists of two florets, *i.e.* spikelet minus glumes. Awn long, twisted and kneed on L.P. of lower floret, and a short straight awn on L.P. of upper flower

SUB-DORSAL OR BASAL AWN

SMALL, ROUND BACK	
Wavy Hair Grass	Larger of the three. L.P. ragged or bifid at apex. Awn twisted and kneed longer than L.P.
Tufted Hair Grass	Mid size of these three. L.P. ragged at apex. Awn twisted and kneed not longer than L.P.
Silvery Hair Grass	Smallest of these three. L.P. bifid. Awn twisted and kneed, twice the length of the L.P.
(Note all the hair	grasses have hair on the rachilla and a basal tuft)

somewhat confused. In order to simplify reading, the parts as named here are tabulated, and some of the equivalents commonly used are placed opposite.

INFLORESCENCE	Ear. Head
RACHIS	Axis of ear. Axis of inflorescence
RACHILLA	Axis of spikelet
GLUMES	Empty glumes. Flowerless glumes. Sterile bracts
PALES	Paleæ. Flowering glumes. Glumellas, Fertile bracts
LOWER PALE	Glumella. Lower or outer glumella. Flowering glume. One-nerved scale. Lemma. Inferior palea. Palet
UPPER PALE	Upper or inner glumella. Palea-pale. Superior palea. Two-nerved scale. Prophyll or bracteole. Valvule
LOWER PALE, PLUS UPPER PALE, PLUS FLOWER	Floret
FLOWER WITH BOTH STAMENS AND CARPEL	Perfect flower, two or bi-sexual flower. Hermaphrodite flower
FLOWER WITH STAMENS ONLY	Sterile, imperfect, or male floret
LODICULES	Scales or perianth of flower. Paleola
AWN	Beard. (Awned grasses are described as bearded)
CARYOPSIS	Grain fruit. Kernel. Berry (of wheat)
" SEED "	Caryopsis only, or C. plus pales, or C. plus pales plus glume plus rachilla, or whole spikelet, depending on type

SEEDS IN GENERAL AND THEIR USE IN AGRICULTURE

Seeds in general enter into agricultural practice in many ways. They are often the ultimate product of the crop and are either marketed as such or consumed directly on the farm.

The " seeds " of the cereal grasses—wheat, barley, oats, rye, maize, and rice—are all one-seeded fruits and provide a great proportion of the total food of the world. In this regard they are closely followed by the true seeds of the pulses—peas, beans, lentils, etc.

Much of the oil used in the world for paint, soap, fuel, lubricant, margarine, and so forth is obtained from crushing oleiferous seeds, such as those of oil-rape, linseed, etc. The residue remaining after oil extraction is often rich in protein and carbohydrate, and comes back to the farmer as a meal or cake for use as cattle-food. Depending on the method of crushing and

extraction, a proportion of the original oil content is found in the residue.

Some seeds, like those of cotton, bear hairs of considerable commercial value. Cotton seed supplies hair for spinning, oil for many purposes, and a valuable cattle food.

On the other hand many " seeds " have a negative importance. Weed seeds occurring as impurities in a marketed product such as grain reduce the value of the material and add to costs when they have to be cleaned out. "Seeds" with adjuncts for dispersal, such as hooks and spines, when lodged in wool are very difficult to remove and also reduce values and add to costs.

Seeds used for Sowing

The most significant aspect of the " seed " in agriculture, however, is to produce a new crop. In this connection the farmer may appear as either buyer or seller. It is when he appears as a buyer that special problems present themselves. When purchasing seed of any kind for sowing the farmer usually has four desiderata in mind.

Firstly, the consignment must be as free as possible from everything other than the seed he wants. In other words, the seed sample should be as pure as possible. When analysed it should show a high analytical purity. There should be few or no weed seeds present nor pieces of useless dirt.

Secondly, as much as possible of the seed of the kind bought should be capable of vigorous germination and produce normally developed plants. The percentage germination should be high.

Thirdly, the plants which develop should possess characteristics inherited from their parents which suit them to the farmer's purpose. The genetical constitution of the embryos in the seeds should be all alike and suitable. They should all be derivatives of a proper strain.

Finally, the seed should be free from disease.

Seed Control

The amount of impurities, weed seeds, dirt, and so on can be evaluated before purchase ; so can the ability of the seed to grow. The presence of disease in the consignment, too, may often be recognized. In most countries, specialist seed analysts ascertain the relevant facts, and the data come before the buyer in the form

PLATE 49 BROKEN SEEDLINGS

The upper photograph shows a type only slightly abnormal: the lower group should be compared with Fig. 93
(*Photo: Messrs. Sutton and Sons Ltd.*)

Soil tests with broken seedlings. (*a*) and (*b*) are equivalent to (*a*) and (*b*) in Fig. 93. Note that plantlet (B) is small owing to loss of cotyledonary food reserve

PLATE 51 CLOVER SEED TYPES

The almost egg-shaped form seen in Crimson Clover, etc.

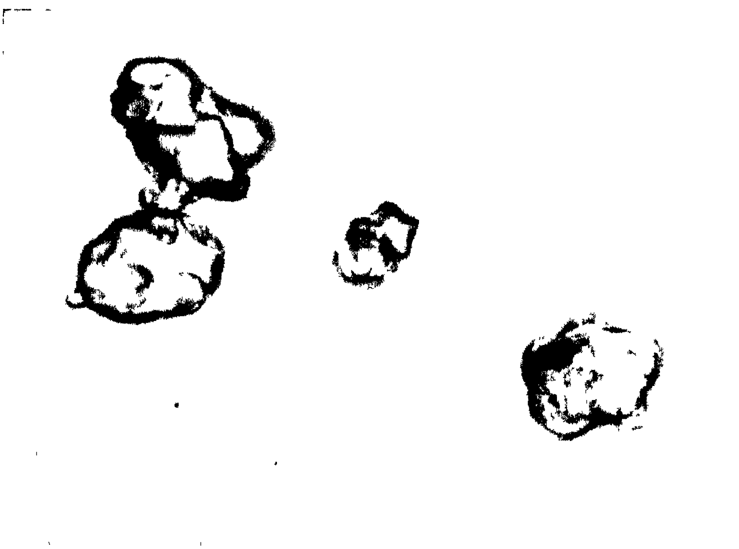
The intermediate shape seen in Red Clover, etc.

The heart-shape typical of White and Alsike Clover, etc.

In shape most Clover seeds fall into one of these three classes

PLATE 52 STARCH GRAINS

Simple grain (one hilum) seen in Potato



Compound grain seen in Rice

of a certificate or declaration presented prior to completion of the purchase. *Caveat emptor,* "let the buyer beware," is an axiom of the common law of purchase and sale in most countries. He has to satisfy himself that the goods purchased are what he wants and worth, to him, the price he pays for them. In many countries the law as regards seeds departs from this idea, and by statute compels the seller to declare to the prospective buyer such particulars as are thought to be necessary and which the farmer by the exercise of reasonable skill cannot ascertain for himself.

Some countries go very far in so protecting the seed-buying farmer. The position in the United Kingdom will serve as an example with which others may be compared. Here, the regulations made under the Seeds Act of 1920 define the position as it applies to sales within these islands. The regulations cover most of the commonly used agricultural seeds both for arable and pasture crops. With only one exception, no part of these regulations prohibits the sale of seed no matter how inferior. They merely insist that the buyer must be given certain significant information regarding a proposed purchase of such kinds of seeds as the regulations apply to.

The one prohibition lies in this, that it is constituted an offence to sell or knowingly sow any lot of seed containing more than five per cent. of injurious weed seeds. These are the seeds of docks, sorrels, species of geraniums, brome grasses, *Holcus*, and wild carrot. All of these which are present are taken together in arriving at the injurious weed seed content of the consignment.

The seller of seed, therefore, must procure all the required information, and this is obtained by submitting to an official seed analyst a sample which in size and composition truly represents the consignment. Official seed-testing laboratories are maintained at Cambridge, Edinburgh, and Belfast. Some of the large seed firms are licensed to carry out official tests for use in their own business.

Seed Analysis

Purity Test

On arrival at a seed analytical laboratory the sender's sample is reduced to a size handy for analysis. This is accurately weighed and is then examined seed by seed. Anything found which is not a complete seed of the kind the sample purports to be is put

to one side. These impurities are then classified in different ways, as, for example, into "other crop seeds," "weed seeds," "injurious weed seeds," and "inert matter." This later class is usually composed of little stones, little bits of straw, empty pales and glumes, etc.

The pure seed and each of the different classes of impurity are then weighed separately. The amount of each in the consignment is calculated as a percentage. It is to be noted that the "percentage purity" in the analyst's declaration is the percentage *by weight* of the seed which the consignment purports, or is declared, to be.

Germination Test

The next step in analysis is for the pure seed to be counted into several small lots, usually individual one-hundreds. These hundreds are then set to germinate under conditions known to be as near as possible ideal for the particular kind. For example, some kinds are placed on a blotting-paper pad supplied with a steady and carefully adjusted water-supply and then kept in an incubator maintained accurately by a thermostat at the "best" temperature. Every seed in the several hundreds is given every chance to germinate. After a definite period under those artificial conditions, the hundreds are examined and the seedlings which have developed counted and destroyed. Any seeds which have not germinated are returned to the incubator and given a further chance. After this second period the seedlings present are enumerated. Thus there are at least two counts for every single hundred. The first count figures for all of the individual hundreds are averaged and noted as the "first count" percentage. The figures of each pad at first count have added to them later those from the second count, and these are also averaged to provide the "total germination" percentage, sometimes called the "final count" or simply the "percentage germination." It is to be noted that the germination percentage is one based on a count, not like the percentage purity which is based on weight.

Special Data Sometimes Demanded

These two figures of purity and germination constitute the principal information the analyst elicits from the sample, and which is conveyed to the sender. Other information has to be given only in special cases laid down in the regulations. For

example, the percentage by weight of "suckling" clover found in the purity test must be declared separately. The *number* of seeds of dodder in a minimum weight of seed has to be declared when present in clover, timothy grass, etc.

"Country of Origin" or Provenance

One other piece of information is required in regard to many kinds of seeds. The seller, when submitting the seed for analysis and to his customers, must declare the "country of origin" or the district in which the seed had been produced. The analyst checks this by noting the kinds of weed seeds present, or the nature of the inert matter found, and should any of it indicate that the consignment has come from an area other than that declared, the fact is reported. The seeds of many weeds and certain kinds of earth or stone are typical of a special country or area, and do not occur in seed produced elsewhere. Attempts at fraudulent representation that a consignment is from a good producing district when in fact it is from an area producing a less valuable strain are controlled to some extent in this way. The method is not infallible. For example, it is well known that at one time certain continental sellers offered red clover seed of Italian origin (not a useful strain in this country) free of indicator impurities. No good seed firm stoops to such fraudulent practice. In some countries (not Great Britain), all imported seeds are stained with a conspicuous dye prior to admission at the ports.

The British farmer, then, when purchasing any of the seeds to which the regulations apply, must be told (*a*) the analytical purity (not in cereals) ; (*b*) the germination capacity ; (*c*) the percentage of injurious weed seeds present ; (*d*) in some cases the country of origin ; (*e*) in some cases the presence of dodder ; (*f*) in some cases the weight of a bushel of seed.

Valuation of Seeds

Having decided on the kind of seed and the country of origin or strain which is to be purchased, the buyer should obtain the analytical data and then examine the seed for himself. The colour should be bright and typical of the kind. This may vary naturally between different consignments. For example, some strains of red clover may be almost butter-yellow, others reddish-purple, while others again are of such a deep purple as to appear

nearly black. In the case of dogstail grass seed, the colour may vary from an attractive bright lemon yellow to a less pleasing deep chocolate. The yellow colour indicates that the seed was harvested in a rather young and somewhat immature condition, and often the chocolate-coloured seed is the stronger in germination and subsequent growth.

The seed should look bright but have no oily shine. It is known that old seed may be improved in appearance by a coating of mineral oil. When oiling is suspected a few of the seeds should be rolled on a piece of clean, white blotting-paper. Oiled seed will leave a characteristic stain.

The smell should be pleasing, and some classes of seed when fresh have special scents of their own. The smell of honey associated with seed of white clover is well known. A sample that smells of mould should be rejected except in the case of Rhenish tall fescue. This seed is harvested on the lands adjacent to the River Rhine and invariably smells of damp or mould. Tall fescue seed which does not smell slightly of mould is probably of an origin other than Rhenish.

The Purity Figure

These points attended to, the purity figures should then be considered. In general, the higher this is the better, but the highest may not be the most satisfactory. Consider three samples each of 95 per cent. purity; in one, the impurities are inert matter of various sorts; in the second, virulent weed seeds; in the third, "other crop seeds" of useful kinds.

It is rare to be faced with a comparison when the decision is so clear cut, but often the nature of the impurities is of greater significance than the purity figure itself. It should be remembered in this regard that what looks like a quite insignificant percentage figure for the occurrence of a weed seed may mean quite a high incidence when sown. For example, it has been computed that one per cent. of dock seed in a grass seed mixture with normal sowing rates supplies ten or more dock per square yard. With a weight percentage such as applies in the purity test, one per cent. of a small-seeded weed in a consignment of a large-seeded crop plant supplies many more individuals per square yard of land sown than does the same percentage when the weed seed is large and the crop seed small.

The Germination Figure

Like the percentage purity, the percentage germination should be as high as possible. The percentage declared is calculated from all the seeds capable of germinating during quite an extended period under ideal conditions. As long as twenty-eight days may be allowed for the germination of such seeds as those of the meadow grasses. The germination percentage indicates the proportion of the seeds in the consignment which are not dead, and is not directly referable to what will happen under field conditions.

Fully viable " energetic " seed germinates promptly under test, and because of its superior vigour may be expected to do better in the soil than a slower lot. The " first count," therefore, may be a better guide to the value of the seed than the final figure.

As an example, consider two samples both having a final count figure of 98 per cent. One shows a first count of 97 per cent. and the other only 65 per cent. There is no doubt which is the better purchase. The figures chosen for the example may be somewhat extreme, but somewhat similar cases do occur.

Swollen Seeds

The nature of the seeds which do not germinate in the test and so reduce the final figure may tell quite a valuable story. If the percentage which merely swelled up and rotted off is high, then the " life force " in the ones which did germinate may be low due to bad harvesting, wet weather, old age, etc. The presence of a high proportion of " swollen seeds " in a test is generally a bad sign. It may be that the " swollen " seeds are quite alive but are " dormant."

Hard Seeds

In clover samples, two other classes of seed may appear in the germination test. The first of them are known as *hard seeds.* These, due to some idiosyncracy of the testa, cannot imbibe water and so remain hard when wetted.

These hard seeds are alive and, if lightly scratched, will subsequently admit water through the abrasion and germination follows promptly. When a seed merchant has a consignment of clover

showing a high percentage of hard seeds, he passes the whole consignment through a cylinder lined with carborundum. This abrades the seed (hard or not), and the percentage of " hards " is reduced to quite a small figure.

There is no doubt that hard seeds, given time, do germinate in the soil, and many authorities consider they should be regarded as at least partially useful. Those of this opinion suggest that a fraction, say one-third or one-half, of the hard seed percentage should be added to the germination final figure. " Hards," in short-term leys at least, germinate too late to establish themselves and compete with the fully grown plants produced by their non-hard fellows. For this reason alone it is probably best to declare the " hards " separately and let each buyer decide their value to him for himself. Other kinds of dormancy are discussed on pages 386 to 388.

Broken Seedlings

The other impurity commonly found in clover seed germination tests is the *broken seedling.* This occurs when the young seedling emerging from the seed coat is seen to be in two or more parts. Some authorities hold that the broken seedling is the product of the more energetic seed, which, stimulated by the too good conditions of the testing station grow so quickly that they shatter. Others hold that the broken seedling is produced by seeds fractured or internally damaged by machining, especially abrasion. Both causes probably contribute. Seeds of trefoil carefully separated from the husks by hand, and quite undamaged, put to germinate at a little too high a temperature with a little too generous water supply will produce broken seedlings. On

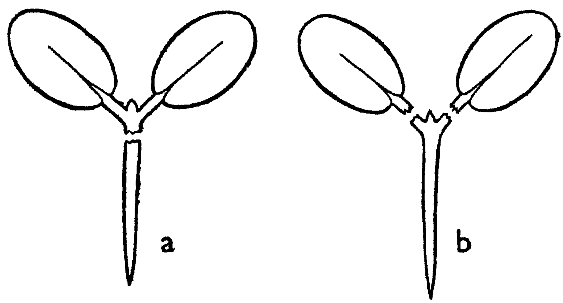


Fig. 93
Points of breakage in broken seedlings

the other hand, it has been conclusively shown that mechanical abrasion of large " bold " seed of red clover does lead to an increase in the percentage of broken seedlings found in subsequent tests. No matter how caused, the practical question turns on the value of broken seedlings if the seed is sown in soil. It is very doubtful if they survive in the rugged conditions of the field seed bed.

Real Value (R.V.)

Having dealt with these various points, the buyer may be faced with the dilemma of choosing between two samples equally attractive, but in one the purity is low while the germination is high ; in the other, both figures are intermediate or reversed in value. How may such samples be compared ? The most useful figure is that known as the Real Value (R.V.) got from the percentage purity figure multiplied by the germination percentage and the result divided by 100. $\text{R.V.} = \dfrac{\text{P} \times \text{G.}}{100}$ This is a percentage by weight multiplied by a percentage by number, and is to some extent fallacious. In actual practice it can be shown that comparisons of the R.V. of samples is quite valid, provided neither of the component figures is abnormally low. So long as the figures are about the levels usual in good-class trade, comparisons by this method are very useful.

Establishment Value

How far is all this information applicable to what takes place in the field ? As regards the purity the main figure has little bearing ; it merely shows up the actual amount of true seed being obtained. One hundred pounds of red clover seed, 95 per cent. pure, supplies only 95 lb. of red clover, and therefore sowing rates must be adjusted accordingly.

As regards the germination figure obtained from the analyst, it should be recognized at once that this merely shows within a small limit of error how many seeds in the consignment are not dead or dormant. It does not indicate how many seeds will germinate and survive in the soil. The proportion of seeds shown as viable by the test and which actually produce plants in the soil is small. This is clearly recognized by practical farmers, who usually sow more seed than is required theoretically. For

example, it is quite easy from the number of viable seeds known to be in a pound of any kind, and the number of adult plants of the same kind that is required to cover an acre, to calculate the number of seeds required to sow an acre in pure stand so that all the land will be occupied.

This theoretical figure is often used in compounding grass seed mixtures in desired proportions, but it is always raised by at least half as much again to allow for deaths and failures. That even such boosted sowing rates are not enough is brought out by the results of experiments detailed in the table on pages 390–391. As is shown, only a few of the larger, more aggressive seeds produce plants near to the theoretical arbitrary figure.

Strain and Country of Origin

The information given in the seeds certificate regarding country of origin implies that seed of the same kind but from different districts may be of different strain and of different value. One country may have the kind of climate that produces a hardy, long-lived, productive strain of plants, while the other has a soft, genial climate which permits the natural selection of less hardy, less productive plants; for example, red clover seed from the hills of Wales compared with red clover from the south of Europe. Information as to the country of origin in regard to many kinds of seed does give a clue to the strain of plants involved, but is subject to a certain amount of qualification and applies more especially where the seed has been produced from truly indigenous plants. When mother-seed from a "hardy" district has been transported to a genial climate, there sown, grown, and used to produce a seed crop, the seed so obtained will be none the worse for the migration and a crop grown from it will show all the characteristics of the original strain. Conversely, seed of a weak, non-hardy strain got through to a seed crop in a less genial area will not produce hardy progeny. In short, seed "once grown" will keep the character of the parents, for natural selection takes more than one generation to produce a definite strain.

Again, good strains of a plant are worth more money than not so good ones, and unscrupulous dealers may substitute one for the other, or mix a proportion of the cheaper with the dearer and omit to make a fair price adjustment or tell the buyer. The

seed analyst can only counter this partially, and the real safeguard for the farmer lies in dealing with a reputable merchant.

Blended Seed

Some buyers throw away what protection they have in this way by buying seed declared to be "blended." It may be that the blend is of the "best sorts," but there is no guide as to the proportion of the "best" present with the "not so good." Blended seed of mixed country of origin cannot be a bargain unless bought at a price as low as the lowest for that kind in the market.

Strain Testing

In some countries the seed control carries this question of strain very much farther. For example, in parts of Europe samples are drawn from consignments as they are delivered to farmers by the retailer, or as the seed lies exposed in the retailer's premises. These samples are sown in trial gardens, and if the plants produced do not conform to description, punitive action is taken against the seller.

A rather better system occurs when some authority such as a governmental agency or a properly organized seed-growers' association recognizes authentic consignments and arranges for their marketing under control. Certification schemes of this nature are common all over the world, and deal with many different kinds of seed.

Cattle-Cakes and Meals derived from Seeds

Seeds are often sold out of agriculture to become the raw material of various manufacturing processes. Common examples are the seeds with a copious fatty reserve which are bought by seed crushers for the extraction of the oil. The interest of the agricultural botanist most usually focuses on these when the residue from such manufacturing processes returns to agriculture in the form of cakes and meals to be used as food for cattle or as organic manures. Cattle foods from various seed sources vary in quality. Some are more valuable than others, and there are price differences between them. Substitution or adulteration of the more valuable by the less valuable may easily be detected by purely botanical methods. In the grinding, rolling, and extraction processes used

on the seeds the fine structure is never wholly destroyed. Usually, the resistant seed-coats or fruit-walls, while reduced to small fragments, are otherwise unaltered. The starch grains, too, often remain quite well defined. Characteristic fibres or hairs, such as those from the epidermis of the cotton-seed, may be still quite recognizable.

Identification of the Seed Source of a Cattle Cake or Meal

Examination of the hand specimen in some cases will establish the presence of certain ingredients. For example, the mahogany-coloured external wall of linseed or the hairs in cotton-seed cake are easily recognized. The smell may reveal others. For example, fenugreek is often added to food quite legitimately as a spice, but sometimes to mask the smell of mould.

Mere examination of the hand specimen is not the end of the matter. For complete confirmation of an identification the material should be subjected to microscopic analysis. This is a large and specialized study, but the principles are capable of brief statement. The small units of the cake are separated out, using water or another suitable solvent. These may be macerated to reveal their fine structure; parts sufficiently large may be selected and sections cut, or starch grains and other cell contents may be isolated. From these, different microscopical preparations are made.

The Shape and Character of Starch Grains

Starch grains from different plants are often very characteristic. They are found in two different forms, simple and compound. Examination of a simple type such as that from the potato shows a shape reminiscent of the shell of the common marine mussel. A dark dot, the hilum, is seen in a position near to what may be likened to the "hinge end" of the mussel shell. A series of concentric lines or striations surround the hilum, following paths parallel with the edge of the grain. This is a very typical starch grain.

If the starch from rice be examined it is seen to be compound. In this case there is more than one hilum present, and each dot is surrounded by its set of striations. The compound grain is in effect a number of simple grains remaining together and forming a "colony."

Structure of Seed-coats and Fruit-walls

Turning to the fragments of seed-coat and fruit-wall which may be present, it will be remembered that the testa is a development of the two integuments of the ovule following on fertilization, while the fruit-wall is a development of the ovary-wall. The changes which take place in these structures may be quite profound. The parts when isolated from the main bulk of the cake or meal may be studied in surface preparation or in section. Usually the most satisfactory section is one perpendicular to the surface of the seed. This, the vertical section, shows the various cell layers of the tissues at different levels, very much as one might see the rooms of a building partially destroyed by bomb damage. In the case of the surface preparation under the microscope, by focusing upwards and downwards, different levels in the structure may be examined. This is equivalent to looking downwards through the different flats of a building with the roof, floors, and ceilings made transparent.

It is not possible here to discuss all the different forms of cattle food which may come into agriculture, but two examples, the first involving a true seed and the other a fruit, will be discussed in order to illustrate the methods used.

The Seed Coat of Beans

Beans of two different genera are used for cattle food in the form of meal. Those are the horse bean and broad bean (members of the genus *Vicia*), as opposed to the haricot and runner beans (members of the genus *Phaseolus*). In vertical section of the testa, the various members of both genera show a very typical construction. It is composed of a number of layers of cells. Each layer is uniform and made up of characteristic elements.

The outermost or surface layer is like a palisade. The individual cells of this palisade are long in the vertical line and narrow in a line parallel to the surface. The lumen of each is reduced, due to wall-thickening, and each contains a well-defined nucleus, with dried-out protoplasm. The next layer downwards is called the columnar layer, and the component elements sometimes called hour-glass cells, because of their peculiar shape resembling the old-fashioned sand-glass. Between each is a characteristic intercellular space. Beneath this there are other layers of cells, none being very characteristic.

Those at least in the deeper layer probably represent persistent elements of the not completely absorbed perisperm and/or endosperm.

Structure of the Testa in Horse Bean

The details of the sections from different beans is revealing. Firstly, the seed-coat of horse bean is quite distinct from all the others, by reason of the size of the individual cells. The coat is about three times as deep in the vertical line as any member of the haricot class.

Structure of the Testa in the Various Kinds of Phaseolus

Comparing the different members of the *Phaseolus* group, the chief interest lies in the columnar layer.

Based on differences in structure of this layer, these beans fall into three main types. Firstly, there are those where the cells of the columnar layer are of the classical hour-glass shape. Five kinds known to occur in trade have so far been examined in this group, and the differences between them are quite distinct and readily recognized in section. The most prominent differences between the members of this group lie in the shape of the cavity of the palisade cells and the arrangement of the hour-glass cells. A second group includes only Burma bean—a poisonous form sometimes the cause of deaths in cattle. Here, the columnar cells are irregular, and are like an hour-glass with the lower bulb cut off. One student has described this layer in Burma bean as like a set of irregular gappy teeth.

The third group is exemplified by the true haricot. Here, the columnar cells have no resemblance either to a column or to an hour-glass, but are cubical in shape. The cell walls are very thin, and the lumen of each cell contains a crystal or crystals of calcium oxalate. It is clear that these beans, very difficult to tell apart in the intact specimen, may be identified quickly and with certainty in microscopical sections of the testa.

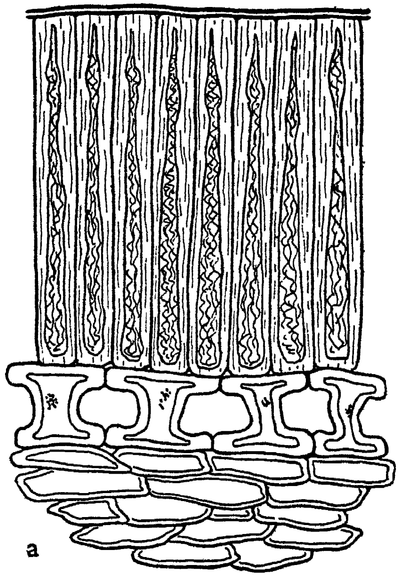
Fruit-walls used in Identification

Turning now to the true fruits which pass as seeds in agriculture, probably the most common examples are the grains for the cereal grasses—wheat, barley, oats, rye, maize, rice, etc. Of these, oats, barley, and unmilled rice are usually invested in the upper

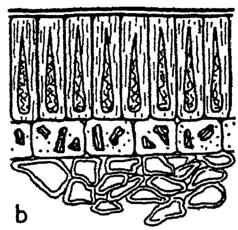
FIG. 94

Microscopic structure of some typical leguminous seed-coats

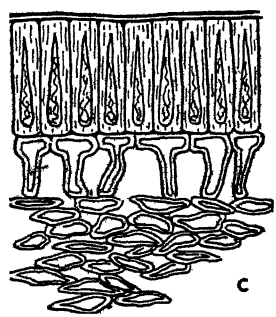
(*a*) Testa of horse bean in vertical section. The whole structure is larger than that of other beans used in cattle cakes or meals. (Note the palisade cells, each with a pear-shaped cavity due to the greater thickening of the walls towards the exterior aspect.) The columnar cells are of a typical dumb-bell or hour-glass shape, thus forming a layer with relatively enormous inter-cellular spaces. The innermost layer is not useful for purposes of identification; it consists of residual endosperm



(*b*) The testa of the true haricot drawn to the same scale. This section is characterized by the columnar cells being cubical, not like an hour-glass in shape, and each contains one or more crystals of calcium oxalate



(*c*) The testa of Burma bean—a close relative of the true haricot. This seed, which is poisonous to stock when fed uncooked, is easily recognized by the characteristic elements of the columnar layer



and lower pales. When the pales have not been milled off they usually provide data for identification of a meal, but the structure of the fruit is usually much more important. Maize is taken here as an example.

The whole grain in maize is about as long as broad, with flat sides. If the grain is laid on the table, one side will show a uniform surface while the other shows a shield-like structure shining through the outer coverings. This is the embryo. A median-longitudinal section of the grain bisecting the embryo longitudinally should be looked at. The main areas are at once recognized, the outer coverings, the embryo, and the endosperm. The coverings are not thick and the embryo is not large. The greater part of the grain consists of endosperm.

The embryo or germ is somewhat difficult to interpret, but in general it consists of a short embryonical axis bearing laterally a shield-shaped structure called the scutellum. This is closely appressed against the endosperm. The scutellum is a suctorial organ. The layer of its cells in contact with the endosperm are full of protoplasm, and when the seed is wetted these release a ferment or enzyme called diastase which is capable of hydrolysing starch. The diastase from the scutellum of the wetted seed passes out into the starchy endosperm, and so makes the food reserves available. The sugar so formed passes from the endosperm into the scutellum, and so to the growing points of the axis. The cells of the main body of the endosperm are simple parenchyma, and each is completely filled with starch grains of typical shape. The outermost layer of cells abutting on the testa, however, are different, being cubical in shape and filled with protein. The protein in this case is not protoplasm, but a simple reserve in crystalloidal form. A peripheral protein-containing layer of this kind is called a aleurone layer.

The layers outside the aleurone layer are composed of the seed-coat and fruit-wall, very much altered from the ovular and ovarian condition. Not only so, but the two are quite adherent, and it is a matter of some difficulty to distinguish where the one begins and the other ends. The aleurone layer plus all the structures of the grain external to it constitute the "bran" and are stripped off in the making of white flour.

Identification of flours, meals, "miller's offals" (bran, wheatings, etc.) from different grains is comparatively easy if characters of the starch, characters of the testa plus pericarp, and so on, are used.

BOOKS FOR FURTHER READING

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SECTION TWO

PHYSIOLOGY

THIS is the study of plant function, the ways in which the plant works, and is based on an understanding of some physical phenomena mainly connected with the properties of particles.

Once these have been explained the mechanism underlying intake of water and other raw materials for food-making or synthesis is dealt with.

The methods by which metabolism, that is, synthesis and respiration, leads to a net increase of dry matter in the plant are then described.

An inquiry into various aspects of growth and development follows. Some plants are shown to be more efficient in a given situation so that there they are able to compete successfully with their contemporaries. The principles of plant competition are then examined with particular reference to growing crops and pastures.

SOME UNITS REFERRED TO IN THE TEXT

millimetre	=	mm.
micron	=	μ (Greek letter *mu*)
	=	$\frac{1}{1000}$ mm.
millimicron	=	$m\mu = \frac{1}{1000}\ \mu$
gram	=	g.
milligram	=	mg. = $\frac{1}{1000}$ g.
microgram	=	μg. = $\frac{1}{1000}$ mg.
		sometimes indicated by γ in place of μg.

millilitre = ml. = $\frac{1}{1000}$ litre and is almost equal to 1 cc.

Temperatures are usually given according to the Centigrade scale. To convert Centigrade to or from Fahrenheit the formula is as follows :

$$F^\circ = \tfrac{9}{5}\,C^\circ + 32\ ;\ \ C^\circ = \tfrac{5}{9}\,(F^\circ - 32)$$

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Chapter IX

FUNDAMENTAL CONCEPTS

To understand the functioning of a plant a knowledge of comparatively simple physico-chemical phenomena is required, and two characteristics of particles are specially important. By particles molecules are here mainly implied, but larger or smaller units will be included in the discussion, as they often show much the same properties.

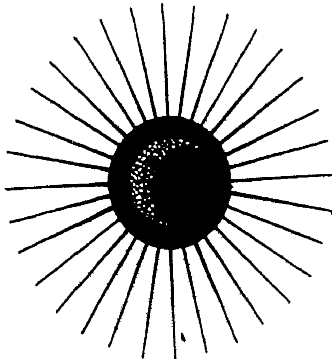


Fig. 95

Representation of a particle with its attraction sphere radiating out in all directions. The strength of attraction diminishes with distance from the particle

The first of these characteristics for mention is that the particles tend to attract each other. The strength of this inter-molecular or inter-particle cohesive force varies with the kind of particle and with the distance between them. All round the particle the force of attraction extends out in what is called the attraction sphere. Within this sphere the strength of the attraction varies inversely as the square of the distance from the particle.

The second characteristic is that particles by virtue of their inherent energy move. Any addition to their stock of energy, as when heat is supplied, increases their mobility. These two concepts of particle cohesion and particle movement must be discussed in some detail.

The Cohesion of Particles

Compare a molecule at the surface of a body of pure water with one down in the main part of the liquid. All round the molecule within the main body there are other similar particles, and so any one of them is equally attracted all round.

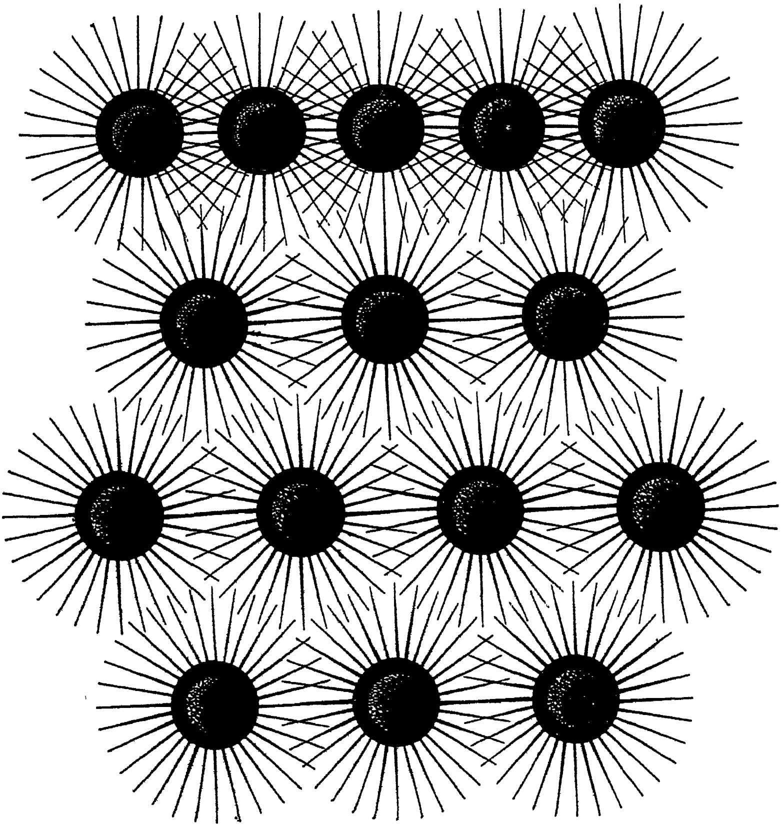


FIG. 96
Representation of molecules of a liquid. Those at the surface are close together, and are held together more strongly than those in the body of the liquid

At the surface of the liquid (gas/water interface), each molecule will be more attracted by its fellow water molecules than by those of the gas. Hence, each one at the surface will have all the attraction force concentrated in the lateral and downward directions with little or none acting upwards into the air. The result is that the layer of molecules at the interface cohere most in the plane of the surface.

Surface Phenomena

That the surface of a liquid has properties different from the main bulk is easily seen when a clean sewing needle is gently placed on it, much as a toy boat might be placed on the surface

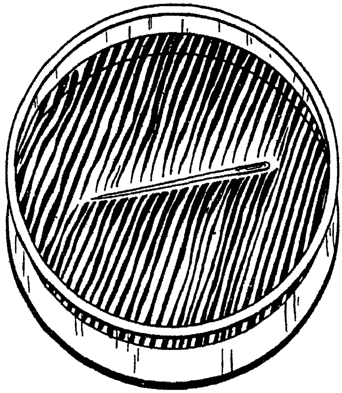


FIG. 97
A needle lying on the surface of water

of a pool. The needle will float. Its weight will press it down into a little hollow, but the surface of the liquid will support it as a sheet of elastic might. If now the needle is gently pushed through the surface layer it will at once sink to the bottom. This demonstrates in a simple way that a peculiar balance of forces occurs at an interface or surface. That these forces are present when all the molecules are alike (pure liquid) is not unimportant, but it is of even greater interest to see what obtains when the molecules present are a mixture of two or more kinds, as, for example, when a second substance is dissolved in the water.

The molecules of some substances are attracted more to water than water molecules are to each other. Other kinds of molecules are attracted less by water than the water molecules are to each other. The presence of molecules of the first kind strengthens the surface film, while those of the second weakens it. This is made visible when a little soap solution is added to the water-surface near to a floating needle. The needle flies away from the side on which the soap is placed. This is because the surface skin on the non-soapy side remains as strong and elastic as it was, while the presence of the soap molecules on the other side weakens the film there. Soap and other substances with similar effect are said to lower the surface tension of the water.

Concentration at a Surface : Adsorption

If a substance which lowers the surface tension is present in the body of the liquid the water molecules there tend to pull towards each other rather than towards the molecules of the dissolved substance. This causes the " intruder " molecules to be squeezed

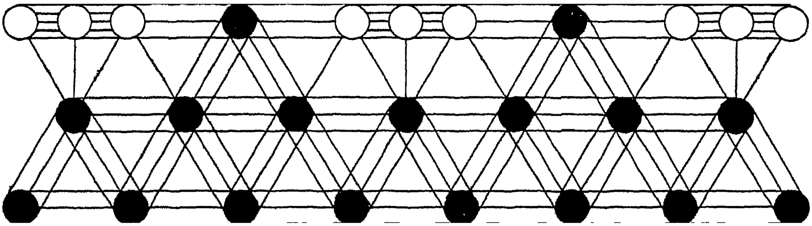


FIG. 98

Representation of the difference in attraction between different molecules causing a surface concentration. The black spheres might represent water molecules W, and the white spheres a substance S dissolved in it which reduces its surface tension

$$(W \longleftrightarrow W) > (W \longleftrightarrow S)$$

out to the surface and concentrate there. A concentration at a surface is called adsorption. The same sort of result may be produced by other means, but this example will suffice for the present. All substances which reduce the surface tension of a liquid adsorb at its air/liquid interface. Such a case is simple, for the gas (air) does not interfere much, if at all, with the forces involved.

At the interface between a solid and a liquid, however, or between two immiscible liquids such as oil and water, the position is not so simple. Here the surface of the solid or liquid may possess additional forces of the same kind. For example, glass attracts water. This is visible where the water in a beaker or capillary tube meets the glass. The surface of the water is concave to the air/liquid interface. The attraction of the glass for the water has pulled it upwards. Indeed, if a capillary tube of sufficiently fine bore is used the attraction of the glass will pull the water up quite a distance against the force of gravity.

What happens when a third substance is introduced? If the glass attracts the particles of the substance more than the water does, then the particles will concentrate at the liquid/solid interface where the water is in contact with the glass. The glass is said to adsorb the substance.

Adsorption, then, is the resultant of molecular attractions and repulsions, and the concentrations which result always take place at an interface.

Desorption

If, when all the particles in the water have adsorbed at the solid surface, the water is drained off and another liquid, which attracts the substance more than the glass surface does, is then

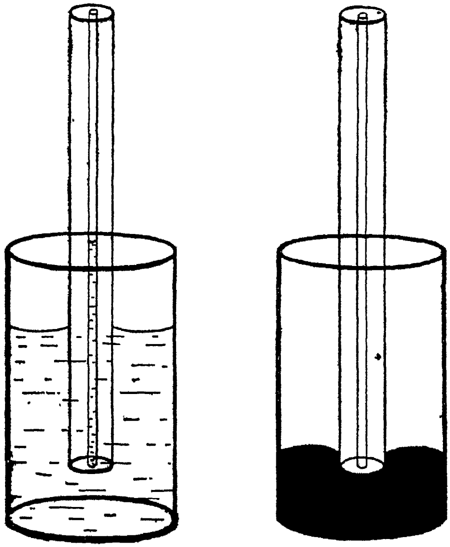


FIG. 99
Position at solid/liquid interface
Left Water/glass. The glass attracts the water and this force pulls the water up against gravity, especially in the capillary tube where the area of contact is great compared with the mass
Right Water/mercury. Glass does not attract mercury

introduced, the adsorbed particles will leave the surface to intermingle with the liquid. The particles are said to desorb. A simple example is seen when a little powdered charcoal (blood charcoal is best) is added to a solution of methylene blue in water. The charcoal adsorbs the blue dye and when the mixture is filtered the charcoal along with the colouring matter is retained on the paper while the water comes through quite clear. If alcohol is now poured over the charcoal on the filter paper the liquid will come through quite blue. Charcoal adsorbs methylene blue from water because it can attract the dye particles more than the liquid does. Alcohol by attracting the blue molecules more than charcoal does causes it to desorb.

Surface Catalysis

Many chemical reactions which take place only with difficulty in ordinary circumstances are speeded up considerably when the two reacting substances are simultaneously adsorbed at a surface.

The material forming the surface does not enter into the reaction, and at the end of the process is recovered unaltered.

When a chemical reaction is accelerated by any agent which itself remains unaltered, the phenomenon is called catalysis, and the accelerator, a catalyst. When a surface is the seat of the reaction the agent is known as a surface-catalyst. It is believed that many surface-catalysts not only expedite, but initiate certain reactions. If this is so, these reactions will not take place in the absence of the appropriate surface. That specific reactions can only take place on specific surfaces is probably connected with a peculiarity of some molecules which are not radially symmetrical; for example, the chain-like forms so often seen in organic substances and illustrated in Chapter I.

Orientated Adsorption

When a chain molecule has groups of entirely different character at either end, the molecule may be adsorbed in a special way. This is seen when the behaviour of a fatty acid in water is compared with that of an almost similar wax (Fig. 100). The CH_3 group is not attracted to water while the COOH group is. The fatty acid molecule is said to show polarity and the attracted group is said to be polar.

At a gas/water interface the fatty acid will be orientated with the attracted polar group in the water, and the remainder of the chain up in the air (Fig. 101). They will "stand" on the surface very much as bottles stand on a floor. The wax molecule added

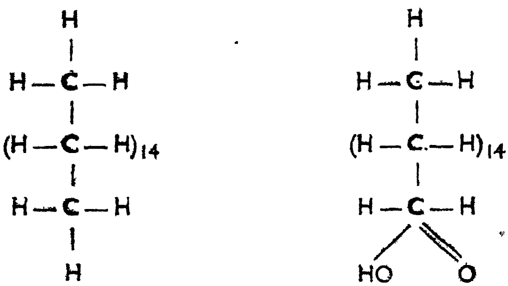


FIG. 100

A wax molecule (left) compared with the corresponding acid (right). Both are long chains with 16 carbon atoms and differ only in one of the terminal groups

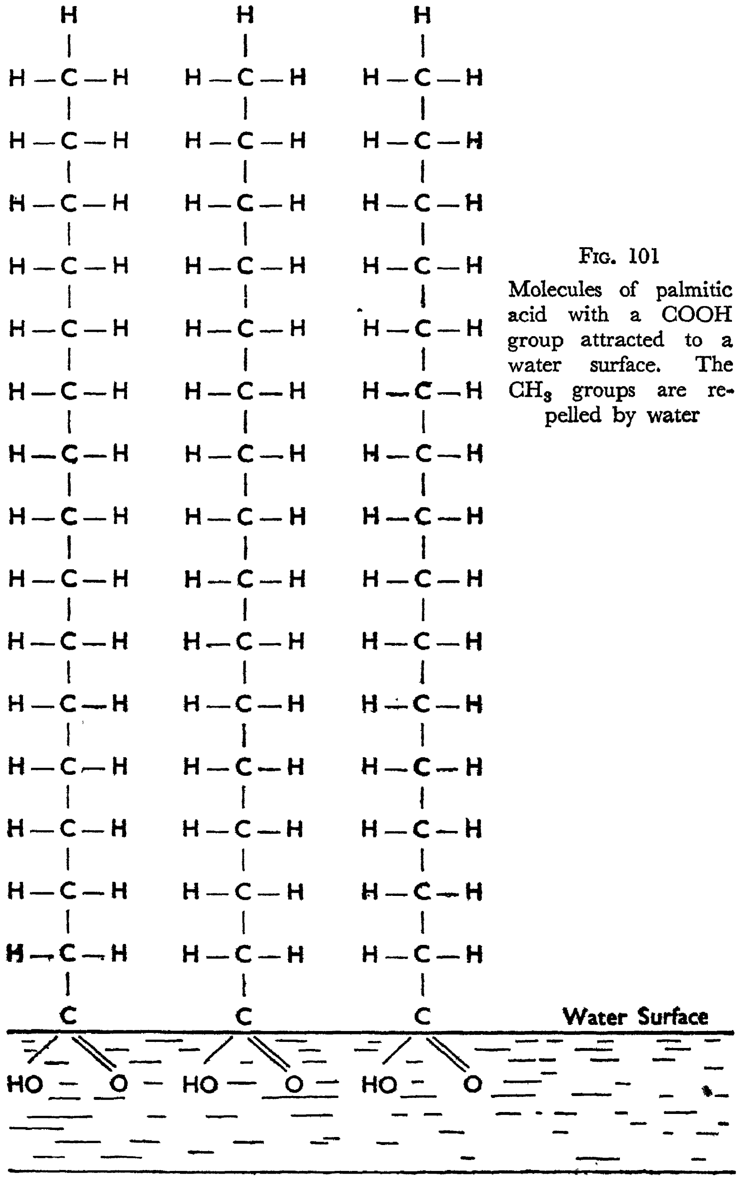


FIG. 101

Molecules of palmitic acid with a COOH group attracted to a water surface. The CH_3 groups are repelled by water

to water will not be orientated at all, but lie " all anyhow " on the surface like a heap of kindling sticks (Fig. 102). Orientation of adsorbed polar molecules takes place in quite a similar manner at solid/liquid and other interfaces.

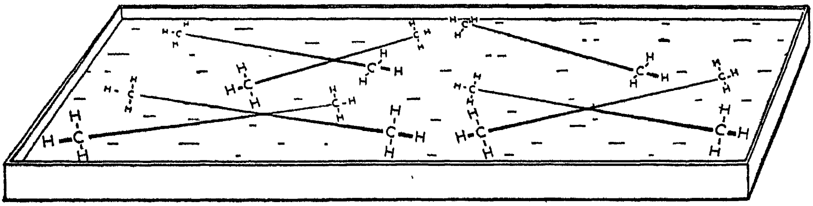


FIG. 102

Wax molecules have no polar group for the water to attract and hence rest on the surface "lying all anyhow." $(CH_2)_{12}$ in each molecule not shown

If different kinds of molecule are adsorbed and orientated at a surface simultaneously, they will always have definite parts of the chain of the one opposite definite parts of the chain of the other. If two lateral groups, one in each molecule, are brought together in this way, any reaction possible between them will be facilitated. The reaction as a whole will then be expedited. By orientation of the molecules, the number of times the reacting groups meet will be increased tremendously over the times they would have met on the basis of pure chance in a mixed solution with the molecules not so arranged.

If the reaction produces a product less adsorbable than the components, it will be desorbed. This will leave room on the surface for more of the two components to be taken on and react. Probably many of the catalysts in plants act in this way, and these are known as enzymes.

Enzymes

Enzymes are specific in the reactions they catalyse. One enzyme, one job, is a nearly invariable rule. Many enzymes have been given names which indicate the work each does with the termination *ase* added. For example, proteases are involved in protein catalyses; amylases with amylum or starch; oxidases catalyse oxidations, and so on. A few of the enzymes discovered in the early days received non-systematic names. Pepsin is a protease.

Reversible Reactions: Equilibrium Mixtures

Many reactions, whether catalysed or not, do not go to completion. For example, a mixture of ethyl butyrate and water gives ethyl alcohol and butyric acid. Equally so butyric acid and ethyl

alcohol react to give ethyl butyrate and water. Either pair produces the opposite pair, and production seems to stop at a definite concentration on each side.

When this point is reached the mixture is said to be in equilibrium. Really the reaction does not stop at the equilibrium point, but continues at equal speed in both directions. Such a " reversible reaction " is usually shown with the sign $\rightleftharpoons$ instead of $=$. In this way the reaction just described would be written: ethyl butyrate and water $\rightleftharpoons$ ethyl alcohol and butyric acid.

In a mixture not at the equilibrium point the speed of reaction is greatest in the direction from the components in greater concentration towards formation of the components in lesser concentration. It so happens that the enzyme lipase which catalyses fat hydrolysis in nature also catalyses this simpler reaction in the test tube. The presence of lipase in the simple mixture considerably reduces the time taken for the initial concentrations to reach the equilibrium point. Its presence does not alter the concentrations at equilibrium. The catalyst only speeds up the reaction, and as it does so in both directions equally, it does not alter the equilibrium point. From this and evidence of a similar character from other sources, it is now believed that an enzyme capable of catalysing a synthesis also catalyses the counterpart, hydrolysis.

Shift of Equilibrium Point

In some reversible reactions, if the enzyme is subjected to alteration of conditions, as, for example, change of acidity or temperature, the equilibrium point shifts. In other words, alteration of the conditions about the enzyme may make it more efficient in one direction than in the other.

This is well seen in the amylases of the potato tuber. These enzymes concerned with passing sugar to starch or starch to sugar are affected as to their equilibrium point by changes in temperature. A potato after freezing for some time is not solid, but is merely a skin containing a sweet fluid, a sugary solution. This potato, if brought slowly from the frozen state back to more normal temperatures, again becomes firm and not sweet. The explanation is this. At low temperatures the amylase enzymes make more sugar from starch than they do starch from sugar; at

higher temperatures they make more starch from sugar than sugar from starch. In short, the sugar $\rightleftharpoons$ starch equilibrium point changes with changes in temperature.

Adsorption is made use of in the plant not just for catalysis but for many other purposes, as will be shown later.

Factors affecting Adsorption

Adsorption depends on a number of factors—the area of the adsorbing surface, the temperature, the specific nature of the adsorbent (the surface), and of the adsorbate (the substance adsorbed), etc. The first factor, namely the area, requires further study at the moment. If the total amount of adsorption in any particular case depends primarily on the area of the surface, then any extension of the area will intensify the possibilities.

Extension of Surface following Sub-division

That a very small amount of a substance can expose enormous surface is exemplified by sub-division. A solid cube of edge one centimetre with its six faces will expose a total of six square centimetres. If the cube is cut along planes parallel to each exposed face a number of cubelets will be produced. If these planes are 10 mμ apart, 1,000,000,000,000,000,000 (10^{18}) cubelets will be obtained. The total area exposed by all the faces of all the cubelets added together will be 6,000,000 square centimetres, or 600 square metres. In English measure this amounts to some 720 square yards, or about one-seventh of an acre. Simple sub-division of the small mass has increased the surface exposed by very many times.

Surface phenomena are intensified in particles at or about the size of these cubelets. This intensification of surface characteristics lessens as the particles become larger or smaller. That is to say, there is a range of size within which particles have special characteristics arising from intensification of surface phenomena.

The Colloidal State

When one substance (phase), divided up into units around this size, is dispersed through another substance or phase the mixture

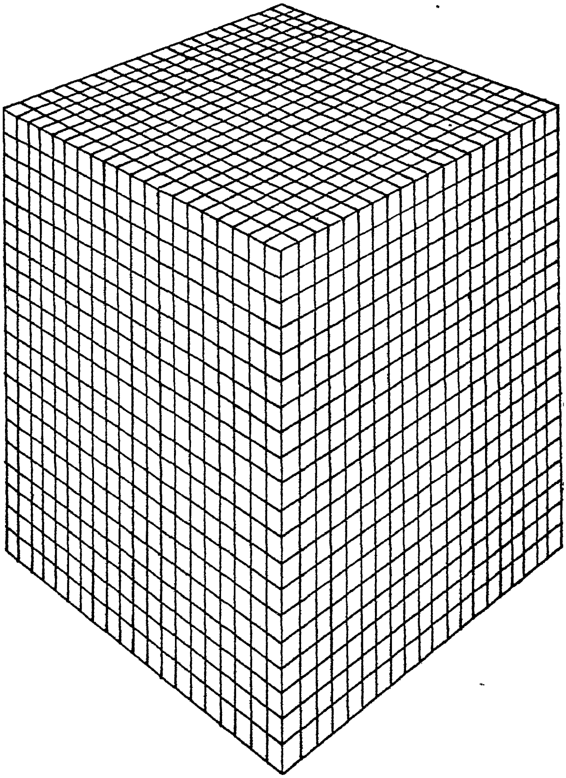


FIG. 103
Subdivision into small parts increases the surface exposed very considerably with no increase of mass

is a heterogeneous system, and is said to be in the colloidal state. In a sense it is wrong to refer to material in the colloidal state as a "colloid," but common use is now establishing the term. There are always two phases in a colloid. The dispersed phase (or micelle(s) or discontinuous phase), being dispersed uniformly through the dispersion medium (or continuous phase or inter-micellar medium).

A " colloid " has been defined by the statement, " a colloidal system occurs whenever one material is divided into another where the subdivision is coarser than molecular." This would not be strictly true, because some of the large polysaccharide molecules and most protein molecules are each large enough to show colloidal behaviour. The whole emphasis in the discussion

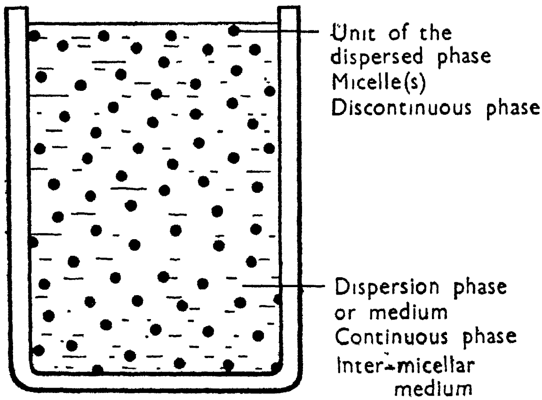


FIG. 104
Representation of a colloidal two-phase system

must come on size of the units of the dispersed phase. The characters of the three possible systems may be summarized in tabular form, as

Small particles	$1\,m\mu$	Intermediate	$0{\cdot}1\,\mu$	Large particles
Molecules and ions		Colloids		Matter in the mass
Not visible in ultra-microscope		Visible in ultra-microscope		Visible in ordinary microscope
Pass through filter-paper and parchment		Pass through filter-paper but not through parchment		Do not pass through filter-paper
When in liquid, a solution		Not a true solution, but do not settle out, *i.e.* resist gravity		Settle out on standing

The lines between classes are shown as muzzy and vague, because, as has already been said, the characteristics of the colloid group slowly grade off towards either of the other two classes as the micelle size is larger or smaller. The actual materials composing the two phases can be gas-in-liquid, gas-in-solid, one liquid immiscible in another, solid-in-liquid, and so on. In the plant the colloids are almost always a solid dispersed in a watery solution, or a liquid dispersed as very small droplets in a similar solution.

Summing up, it may be said that in the colloidal state a

very small mass dispersed in extremely small units exposes to the dispersion medium a very large area of surface; that this surface has great potentiality; and that the major portion of the plant body is in the colloidal state.

Kinds of Colloidal System

The relationship between the phases may now be mentioned. When the dispersed phase adsorbs the dispersion medium the colloid is said to be *lyophilic* (solution-loving). Where water is the dispersion medium the narrower term *hydrophilic,* or water-loving, is used. Where the dispersed phase does not adsorb the dispersion medium the term *lyophobic* (solution-hating) or *hydrophobic* (water-hating) are used.

This relationship is important. A hydrophilic colloid can retain water tenaciously; it binds it, and so we speak of bound water. The amount held depends on circumstances. If the capacity of a colloid for water is fully satisfied, the surface of the micelles will be fully covered to some depth and the colloid is said to be fully hydrated or saturated. Any stage less than full saturation is one of partial hydration. As a hydrated colloid progressively dehydrates under drying conditions the "skin" of water round each micelle becomes thinner and thinner, and each successive portion of water remaining is held with increasing tenacity. The closer an adsorbed water molecule is to the adsorbing surface the more strongly is it bound.

Many surfaces can be shown to carry an electric charge, and this is true of the surface presented by colloidal micelles. When particles carrying a charge of sign opposite to that borne by the micelles are introduced into a colloidal system the micelles are attracted to them. They "bunch" together and form large units. This formation of large units destroys the colloidal system, for matter in mass is formed. Many colloids precipitated in this way do so in clots like flock. They are said to flocculate. A hydrophilic colloid is very stable, for in it the envelope of bound water tends to prevent the micelles from coming in contact, and they do not readily run together and precipitate out or flocculate. The introduction into a hydrophobic colloid of a very few particles carrying a charge of opposite sign to that borne by the micelles is sufficient to flocculate a large volume of colloid. Hydrophilic colloids are stable; hydrophobic colloids are sensitive.

Sols and Gels

Some colloids flow or pour like liquids, and therefore suggest a solution; these are called "sols." Other colloidal systems resist deforming forces to some extent; they resemble a jelly and are called "gels." Sols can be converted into gels and vice versa. A table jelly when hot and ready for pouring into moulds might be described as a nearly fully hydrated hydrophilic sol, and once it has cooled and set, as a nearly fully hydrated hydrophilic gel.

Relating these general facts to what is found in the plant it is safe to say that the cell-walls, the protoplasm, the nuclei, mucilages (when present), and many other components are in the colloidal state. In fact, the greater part of the body of the living plant is composed of organic material dispersed in water.

Movement of Particles

Passing to the other aspect of the nature of matter mentioned at the commencement of this chapter, it may be said that all particles below a certain size are capable of movement. The two forces, inter-molecular attraction and power of movement, are in effect opposed to each other.

In a solid, the speed at which a molecule may travel and the distance travelled in a straight line are both restricted by cohesion. In a liquid, movement is freer, because intermolecular attraction is decreased. In a gas the individual molecules attain their greatest degree of freedom with least cohesion.

This ability of particles to move can be made visible. If a "dilute" suspension of an insoluble, very fine powder (*e.g.* carmine) in water is observed under the high power of the microscope, the particles will be seen to vibrate. They go off in one direction, travelling in a straight line, then change direction sharply at an angle and continue on the new path for a time, only again to alter course sharply. With careful observation it will be seen that small individuals travel faster than large ones. The speed at which they travel is inversely proportional to their size. Further, if one particle is selected for observation and each excursion it makes in a straight line plotted, it will be seen that there is an average length of path in a straight line. This is called the mean free path. It is called the free path because

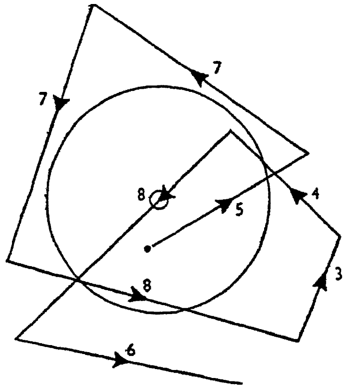


FIG. 105
Representation of the track of a particle in a homogeneous mixture. The particle vibrates about a fixed point. The "mean free path" is indicated by the circle. The numbers indicate the relative lengths of the paths

change of direction is caused by collision with another particle which may not be visible. The length of the path depends on the concentration of the particles; the more particles there are per unit of volume the oftener will a particle collide with another.

A particle, therefore, if small enough moves; it travels in straight lines; movement in any direction continues until it collides with some other object, such as another particle or the walls of the containing vessel. The particles may be visualized very much as billiard balls in constant motion cannoning off each other and the sides of the table. The actual system, however, is three-dimensional.

If the other particles are evenly distributed all round the individual under observation, it will collide after about the same distance travelled no matter what direction it takes. This means that if the dispersion of the particles is uniform throughout the system, the free path of each particle extends equally in all directions and will vibrate round a fixed point.

On the other hand, should the particles not be uniformly distributed in the system there will be greater chance of any one colliding with another when it travels toward an area where there are more of its fellows—that is, into an area of greater concentration. When, however, such a particle travels towards an area where there are fewer of its fellows—that is, into an area of lesser concentration—there is less chance of a collision. This will reduce the length of the free path in one direction and increase it in the opposite direction. Thus, instead of seeming to vibrate about a fixed point, as the particle does in a uniform concentration, it will tend to move away from the area of greater con-

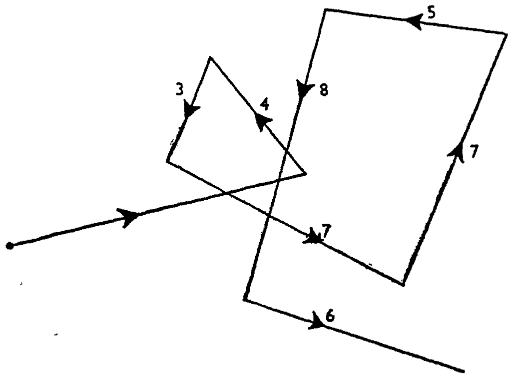


FIG. 106
Representation of the track of a particle in a non-homogeneous mixture if the concentration is greater towards the left and less towards the right

centration towards the area of lesser concentration. A movement of particles in this manner from an area of higher concentration to an area of lesser concentration is known as diffusion.

Temperature and Viscosity in Relation to Particle Movement

If energy is supplied to the particles (as by heating) they will move faster. At temperatures at which the living plant can function, say from about freezing-point to perhaps 35° or 40° C., the increase of speed is not of much significance. If a series of microscopical preparations of carmine is made not in pure water but in gum arabic solutions of strengths 1 per cent., 3 per cent., and 5 per cent., it will be seen that the rate, and mean free path, of each particle are in inverse proportion to the strength of the gum. The viscosity of the gum restricts the activity of the particles. When these preparations are gently heated the speed of the particles rises very steeply, and the mean free path becomes very much longer. The rise in temperature reduces the viscosity of the gummy liquid considerably, and in this way reduces the "drag" on the particles, giving them greater freedom of movement, and therefore increasing diffusion. Diffusion in the plant is greatly expedited by a rise in temperature, which reduces viscosity.

SOLUTIONS

Consider now "mixtures" of another type—solutions. Solutions are composed of a solid, a liquid, or a gas (the solute) in a liquid (the solvent). The liquid is the solvent, the substance dissolved in it is the solute. The universal solvent in living material is water.

A solution is intermediate in character between a chemical compound and a mechanical mixture. The line of demarcation between a mixture on the one hand and a chemical compound on the other is not simple. A chemical compound involves molecules or smaller units, and the components always unite in constant proportions. The result of the union possesses properties which are not the sum of the components. A mixture involves particles larger than molecular, and the components mix in all proportions, the resultant takes on no properties not the sum of the components. In a solution the particles of the solute are molecules or smaller units. The proportions in which they permeate the solvent are not constant, but the " mixture " takes on properties different from the sum of the components. The only solvent which need be considered here is water, as it is the universal solvent in living plants.

Solubility

When a substance is placed in contact with water, molecules may pass out into the solvent. If this happens the substance is said to be soluble in water. If no molecules pass out, then it is insoluble. The degree to which any solute is soluble in water depends on the specific nature of the solute ; some are more soluble than others.

Ionisation

When some solutes, particularly electrolytes, are placed in water a proportion of the molecules in the water are found to exist as charged " fragments " or particles called ions. For example, sodium chloride (NaCl) in solution yields two ions, a sodium ion Na^+, and a chlorine ion Cl^-, and the salt molecule may be regarded as split or dissociated in solution. The ion, like its parent molecule, behaves as a particle, with the result that in a solution of sodium chloride there are nearly twice as many individual particles as would have been present if the salt had dissolved as a complete molecule.

Acids and Bases

Before going on to inquire into solutions further one aspect of dissociation may be dealt with. All liquids of which water is one of the components contain some positively charged hydrogen

ions (H^+), and some negatively charged hydroxyl ions (OH^-). When each of these is present in exactly equal numbers the liquid is neutral in reaction. If there is an excess of hydrogen ion present, the liquid behaves as an acid, and if there is an excess of hydroxyl ion it behaves as a base. The concentration of ion is always small. It is important to note that the products of the concentrations $C_H \times C_{OH}$ is a constant, and amounts to $10^{-14 \cdot 14}$ at 18° C. Hence if the concentration of either the H ion or the OH ion is known, that of the other is easily calculated. In practice only the hydrogen ion concentration (H.I.C.) is estimated.

Hydrogen Ion Concentration and the Symbol pH

The figures expressing the number of H ions per unit volume are very unwieldy to write or to say, and the hydrogen ion concentration is usually shown by the index of the actual H.I.C. with the negative sign changed to positive. This quantity is represented in writing and often referred to in speech as *p*H. The *p*H of pure water (H.OH), which on dissociation provides an equal number of both ions, and is therefore neutral, is 7·07. In biological work this is taken as 7.

Adding an acid to pure water increases the acidity, or H.I.C., but owing to the method of calculation lowers the *p*H. Adding a substance dissociating to yield OH lowers the H.I.C. and raises the *p*H. The *p*H scale thus extends upwards and downwards from neutrality at 7. A *p*H of less than 7 denotes acid, while one greater than 7 denotes alkaline conditions.

A rise by one whole number in the *p*H scale represents an H.I.C. one-tenth of the concentration of the preceding whole number. Intermediate values are shown by decimals. Each increase of 0·1 in *p*H represents 20·56 per cent. decrease in H.I.C.

Measurement of Hydrogen Ion Concentration

Many coloured organic compounds called indicators change from one colour to another with change in H.I.C. They "indicate" over a more or less narrow band of the *p*H scale. These are used to estimate H.I.C. A series of these different-coloured compounds can be assembled separately, each individual "indicating" at different levels of the *p*H scale. A mixture of indicators from this series can be made up which will change colour pro-

gressively over a quite wide range of pH. Such an omnibus indicator is known as a universal indicator.

It is interesting to note in passing that many of the beautiful colours produced in plants and many of the changes seen in opening flowers, ripening fruits, and autumnal foliage are due to substances in the plant " indicating " changes of H.I.C.

Buffer Action

Substances which when present in a solution take up hydrogen ion or hydroxyl ion by adsorption or chemical action, prevent sharp changes in H.I.C. occurring if acid or alkali is added. These substances are known as buffers. A well-buffered solution will move very slightly up or down the pH scale on addition of quite large amounts of acid or alkali.

DIFFUSION

Returning now to the further consideration of a soluble substance placed in water. It was said that some of its molecules fly off into the liquid—that is, they go into solution. Some of these may be dissociated, but the essential point here is that particles (molecules and/or ions) become free in the water. These particles are mobile, and vibrate quickly in a manner quite similar to that seen in the carmine suspension. They are capable of diffusion. The number of molecules which go into solution in given time depends primarily on the degree of solubility of the substance in the water. Solubility, then, conditions the number of molecules which move out at one time into the solvent. This can be visualized as the number which can " move abreast " in the liquid, and is called the diffusion front. With a highly soluble substance this diffusion front will contain many molecules and diffusion will

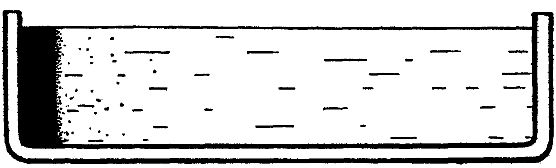


FIG. 107

A sheet of substance just after its introduction into a trough of solvent in which it is soluble. The first molecules are going into solution

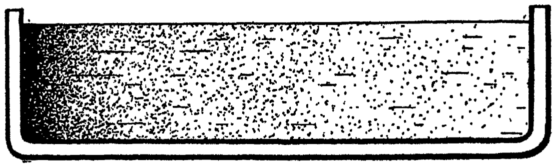


FIG. 108

The same as Fig. 107 after diffusion has gone on till the diffusion front has reached the farther end of the trough

be rapid. With a low solubility the number in the diffusion front will be low, and diffusion consequently slower.

Behind the front other molecules will continue to fly off, and collide with those in advance of them. The difference in number of molecular collisions behind and in front of any molecule will cause it to be impelled forward. This movement of particles outwards into the liquid will continue, and more and more molecules will leave the solute surface. The position may be represented, as in Fig. 107. If, when the front reaches the farthest limit of the liquid, samples of the solution are drawn simultaneously at a large number of points between the two extremes, and the concentration of the solute molecules estimated for each sample, then on plotting these concentrations a curve something like Fig. 109 will result. The curve shown is ideal, and would change in detail with different solutes.

A Diffusion Gradient

This sloping line is a visual representation of what is called a concentration gradient or "gradient of diffusion." Just as a gradient on land can be defined as the difference in level between two points divided by the distances between them, so may the

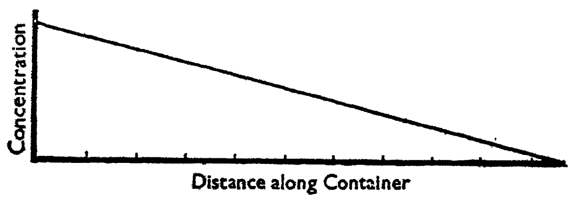


FIG. 109

Ideal curve of concentration in a diffusion gradient

The concentration of solute plotted against distance for the case shown in Fig. 108 above

gradient of diffusion be defined as the difference in concentration between two points, "C_1 and C_2," divided by the distance "D" between:

$$\text{Conc. gradient} = \frac{C_1 - C_2}{D}$$

The process of diffusion goes on until the gradient ceases to exist, that is, until the solution is homogeneous and the concentration of the solute is equal throughout. When this state is reached any solute molecule will collide with its neighbours equally all round. When the molecular (particle) concentration of solute is equal throughout the liquid, diffusion equilibrium is established.

Factors affecting Diffusion

The speed of diffusion depends on four factors. First, there is the dissolving power of the solvent for the solute, already mentioned. Secondly, there is temperature, and this in plants acts most significantly, not by increasing the energy of the particles, but by reducing viscosity or frictional resistance of the solvent. Thirdly, there is the size of the diffusing particles. With small molecules at constant temperature half the mass of the molecule multiplied by its velocity squared ($\frac{1}{2}mv^2$) is a constant, *i.e.* "the speed of diffusion is inversely proportional to the mass of the molecule."

With large molecules and aggregates of molecules (colloidal micelles) this hardly holds, because surface effects interfere, and the rate of diffusion in these cases varies inversely as the radius of the particle. Finally, and most important for the studies made here, there is the steepness of the gradient. Assuming a simple case—take a section through a diffusion system.

S = amount of solute passing through the plane or area A in time t, x is the distance between the two different concentrations C_1 and C_2. Then $\frac{s}{t} = Da\frac{C_1 - C_2}{x}$

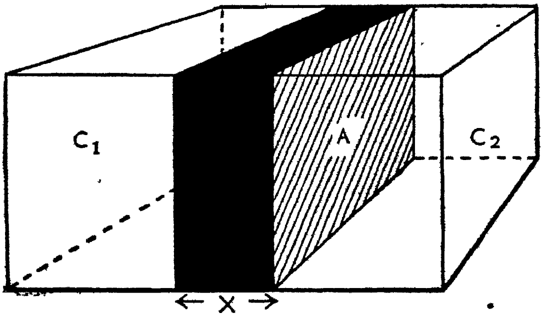


FIG. 110
Section through a diffusion system

For this to be valid, the relationship between C_1 and C_2 must remain constant, but as in diffusion one is falling and the other rising, the position may be restated as $\frac{ds}{dt} = Da\frac{dc}{dx}$

D is the coefficient of diffusion, the quantity of solute passing across unit area in unit time when the concentration gradient is unity. It is, of course, independent of the degree of concentration involved, but varies considerably for different substances. In general, D is high for simple inorganic molecules and decreases in value as the molecule increases in complexity. It is extremely low for substances of high molecular weight or aggregates of molecules such as colloid micelles.

The Solvent Diffuses as well as the Solute

Further consideration of Figures 107 and 109 used to illustrate the gradient of the solute shows that the solvent too differs in concentration in different parts of the system. Just as the solvent molecules dilute the solute molecules so do the solute molecules dilute the solvent. The solvent diffuses from its area of higher molecular concentration to its area of lower concentration and in a direction opposite to that of the solute. The complete graphical representation of the concentrations in the system should be as seen in Fig. 111. In short, there are two gradients : one of the solute and the other of the solvent. These two gradients do not affect each other except in so far as by their action they alter concentrations. The components of a diffusion system move down their own particular gradient quite independently of each other.

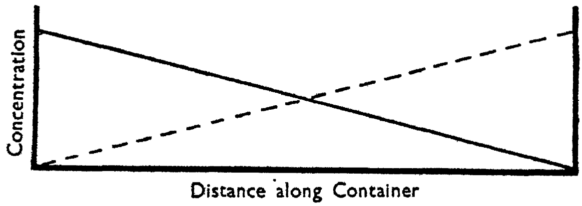
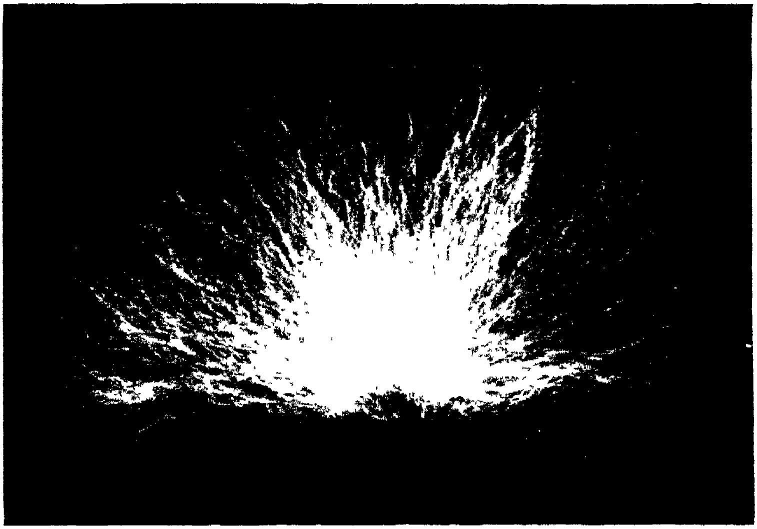


FIG. 111

Ideal curve of concentration in a diffusion system to show position of solvent and solute for the case shown in Fig. 108 above

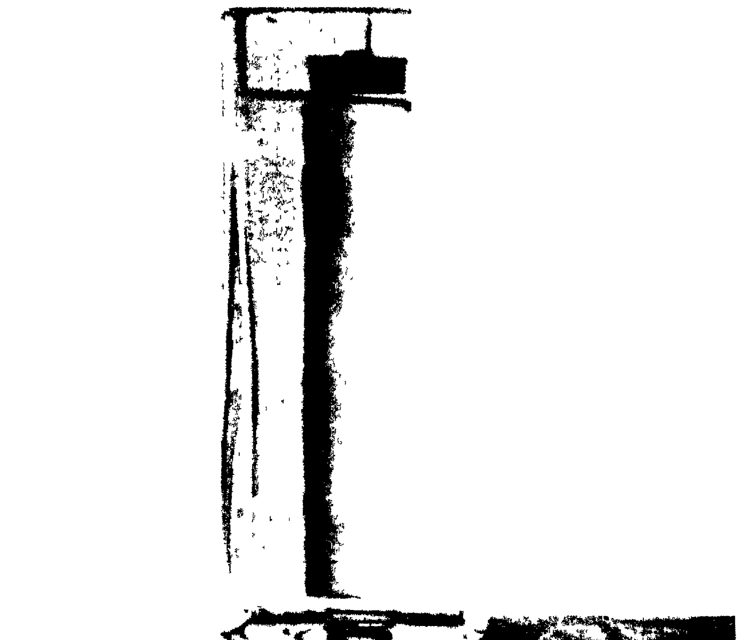
Concentration of solute ————
Concentration of solvent — — — —



The seed of Cotton bears epidermal hairs

The "seed" of Maize is a one-seeded, dry, indehiscent fruit with the fruit wall transparent and adherent to the seed coat. The shield-like area is the scutellum, a part of the embryo

PLATE 54 TRAUBE CELL



A hollow cylinder of porous porcelain has a semi-permeable membrane formed in the pores. Inside the cylinder is a solution of cane sugar, outside there is pure water. Water molecules diffuse in, and the fluid rises in the tube creating a hydrostatic head

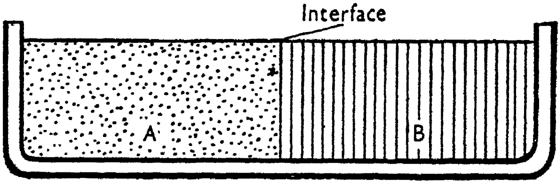


FIG. 112
Because solvent A dissolves the solute, concentrations become uniform throughout. The solute is insoluble in solvent B and no solute enters that section

Diffusion in a Heterogeneous System

Let another component be introduced into the system, say solvent B as in Fig. 112. There is now the original solvent A and the new solvent B. Let it be assumed that the two solvents do not mix. The solute diffuses as before in A until it meets the surface of B, the interface between the two liquids. If the solute is insoluble in B it will not pass into or permeate B but will diffuse into A, or, in other words, permeate A until the concentration is uniform throughout A. In such a case A is said to be permeable to the solute while B is impermeable. If, on the other hand, the solute is soluble in B it will cross the interface and diffuse on and permeate B. In this case, both solvents are said to be permeable in regard to the solute. The concentration of solute (degree of permeation) in the two solvents at equilibrium may be different, for it depends on the dissolving power of each particular solvent for the particular solute.

Semi-permeability

Suppose now a situation where a section or septum of B divides two portions of A (A_1 and A_2 in Fig. 113). Again the solute will diffuse out through A_1 till it reaches B. If insoluble in B (B im-

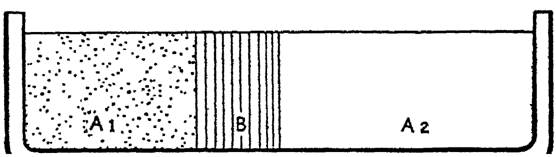


FIG. 113
The solute is soluble in A but not in B, hence two regions of Solvent A (A_1 and A_2) exist with quite different concentrations

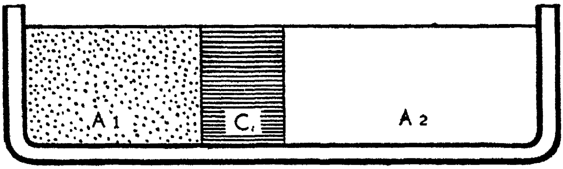


FIG. 114

The same conditions as in Fig. 113 but solvent C replaces solvent B. Solvent C cannot dissolve the solute but is miscible with solvent A. Hence A diffuses from its area of higher concentration A_1 to its area of lower concentration

permeable) the solute will remain in A_1 and diffuse in it till the concentration is uniform there, so that the sections A_1 and A_2 will have very different molecular concentrations. Next suppose that instead of solvent B another solvent, C, is used, which does not dissolve the solute (is impermeable to it) but dissolves (is partially miscible with) solvent A. Now one section of A diluted by solute molecules is separated from the other undiluted section by a septum of C. There is a concentration gradient of solvent A across C from A_2 to A_1. As solvent A can mix with (permeate) C, diffusion from A_2 to A_1 will take place. Solvent C is thus permeable to one component (solvent A) of the system and impermeable to the other (the solute). Such a septum or membrane is said to be semi-permeable. A septum such as C is a membrane—a semi-permeable membrane—and the diffusion through it of solvent only is called osmosis. Osmosis is defined as the diffusion of the solvent of a solution through a semi-permeable membrane.

There are two kinds of semi-permeable membranes. Those completely impermeable to all solutes but freely permeable to the solvent are described as perfect semi-permeable membranes. Those membranes which are impermeable to some solutes, but are permeable to others in some degree, are the so-called imperfect semi-permeable membranes.

The Two Factors Conditioning Semi-permeability

This explanation of permeability based on differences of dissolving power explains the vast majority of cases of osmosis.

When the membrane (solvent C of the diagram), however, is colloidal, a slight complication occurs. The colloidal membrane may be pictured as something like a filter or sieve, the spaces between the micelles being equivalent to the spaces between the

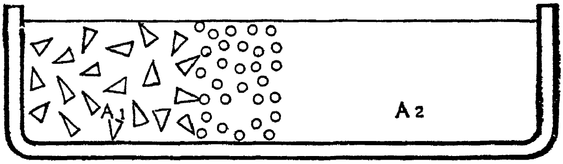


FIG. 115

Representation of a colloidal membrane impermeable to a solute molecule too large to pass through the intermicellar spaces

gravel or silt of the filter, but of very fine diameter. In different colloids, or in the same colloid under different conditions, the inter-micellar space differs.

For a particle to diffuse through a colloidal membrane it must satisfy at least two requirements. The particle must be capable of dissolving in the dispersion medium, and it must be small enough to pass between the micelles. A colloidal membrane is permeable only to particles which dissolve in its dispersion medium and at the same time are of a size smaller than the spaces between micelles.

The Demonstration of Osmosis

An example of the kind of system used in demonstrating osmosis is the Traube cell. In this apparatus a porous pot is used to support the delicate membrane or the actual equivalent of solvent C of the figures just discussed. The membrane is constructed by filling a hollow cylinder of porous porcelain with an aqueous solution of copper sulphate, and then immersing it up to the rim in a solution of potassium ferrocyanide. The two solutes move through the pores of the porcelain and meet at the middle of the wall, where they react chemically to form a membrane of copper ferrocyanide. Copper ferrocyanide is a very good semi-permeable membrane, and when supported within the pores of the porcelain pot, can be handled easily and withstand hard mechanical usage. A rubber cork pierced by a glass tube may be inserted in the mouth of the pot. If the cylinder is filled with an aqueous solution of cane sugar and the pot immersed in pure water or an aqueous solution of lower solute content than that inside, all the conditions as shown in Fig. 114 are satisfied.

Copper ferrocyanide is not permeable to cane sugar but is permeable to water, so there is a functional diffusion gradient of water in the direction running from outside inwards.

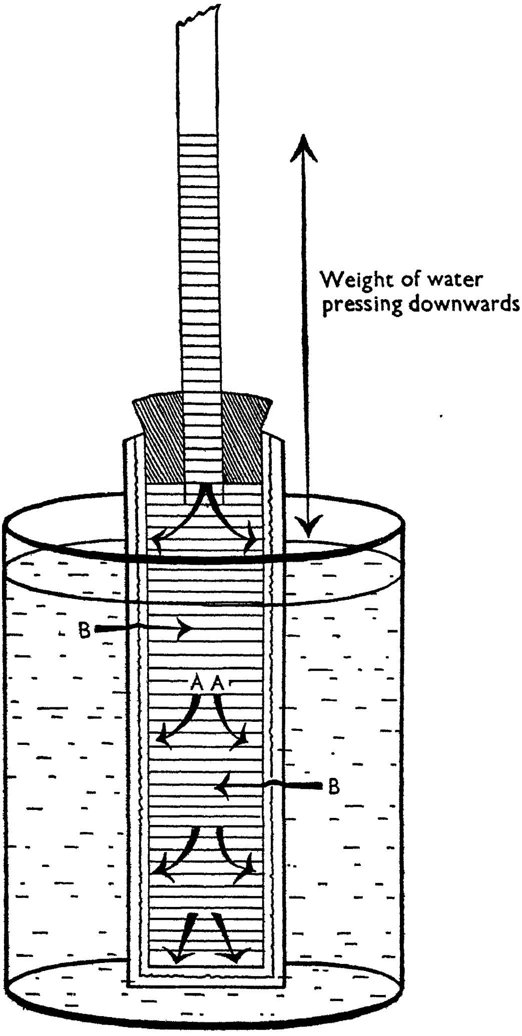


FIG. 116

Section of Traube cell

The arrows B inwards suggest the diffusional movement, the arrows A pointing down and outwards suggest the hydrostatic head pressing water out

Osmotic Pressure

Water molecules diffuse into the pot, which is already quite full to the cork. The liquid is practically incompressible, hence it must rise up the tube against the force of gravity. In time, a column of liquid will occupy the tube. Such a column has weight, and will exert a hydrostatic pressure downwards and outwards on the liquid in the pot. This will press molecules of water out of the pot back into the outer vessel. As the liquid

rises higher the hydrostatic pressure will increase, and more and more molecules will be pressed out. The column will rise more slowly as the number of molecules pressed out approaches the number coming in by diffusion. When the column has risen to such a height that the hydrostatic head presses out as many molecules of water as enter by diffusion, the column will rise no higher and the system will be in equilibrium. At this point the value of the hydrostatic head may be expressed in appropriate units. No matter how expressed, the figure obtained is a measure of the osmotic pressure. Any method by which a pressure is impressed on the liquid inside the membrane will have the same effect. Merely sealing the pot with an intact (not pierced) cork instead of one carrying a glass tube will have this effect, for as solvent enters, the pressure inside the pot will rise. The rigid walls will press back on the solution and so press out solvent molecules until equilibrium is attained. Osmotic pressure is therefore defined as the equivalent of the pressure which must be imposed on a solution to maintain its volume constant when it is separated from the pure solvent by a perfect semi-permeable membrane. An apparatus of this type used to demonstrate osmotic pressure is called an osmometer.

Exosmosis and Endosmosis

The passage of solvent inwards in this manner into the porcelain pot or cell is sometimes called endosmosis. This term has little importance as it is used merely in contradistinction to exosmosis, the outward movement of solvent which occurs when a higher concentration of solute (lower concentration of water) is placed in the outer vessel. Such a reversal of the gradient reverses the direction of diffusion and water leaves the pot to enter the outer solution.

BOOKS FOR FURTHER READING

FINDLAY, A. *Introduction to Physical Chemistry* (Longmans, Green & Co, London, New York, Toronto, 1941)

GORTNER, R. A. *Outlines of Biochemistry* (John Wilerys & Sons, New York; Chapman & Hall, Ltd., London, 1929)

CHAPTER X

OSMOSIS IN THE LIVING CELL; TURGOR

THE PHYSICAL FORCES IN A PLANT CELL

THE passage of water from the soil into the root and from cell to cell in the tissues is effected entirely by diffusion and largely by osmosis.

In order to simplify discussion consider first an isolated parenchyma cell dissected out of a plant and immersed in water. The cell-wall is completely permeable except to large solute molecules. The living protoplasm is an imperfect semi-permeable membrane. The cell sap is largely a solution of salts, sugars, organic acids, and other soluble substances. The dissolved substances of the vacuole *as a whole* reduce the concentration of water molecules in the sap. There thus exists a gradient for water into the cell. Water diffuses in and the volume of sap increases. This presses the protoplasm outward against the wall. The wall presses back. This inwardly directed pressure of the wall is a force impressed on the solution in the vacuole. It must therefore force water molecules out of the cell just as did the hydrostatic force in the artificial Traube cell, described in the previous chapter. When the wall pressure forces out of the cell as many

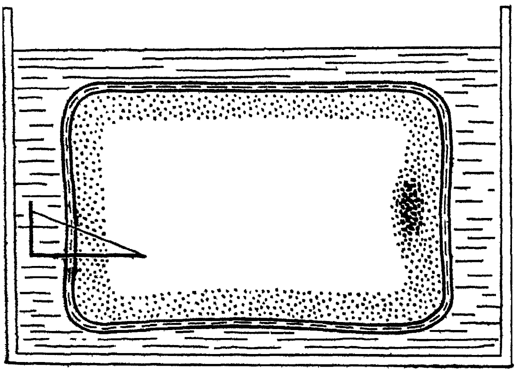


FIG. 117

A parenchyma cell isolated and placed in water. There is a diffusional gradient of water inwards

molecules as are coming in by diffusion, the cell gets no bigger and equilibrium is established. In this state, when no further increase in water-content or volume is possible, the cell is said to be turgid or in a state of turgescence.

There are thus four forces recognized in a cell in equilibrium :

(*a*) The osmotic value of the solution outside when it is not pure water

(*b*) the osmotic value of the liquid in the vacuole

(*c*) the inwardly directed force of the wall

(*d*) the resultant of these forces which is force *b* minus force *a* minus force *c* or : $d = b - (a + c)$.

In an intact tissue, force *c* is reinforced by the pressure of neighbouring cells.

The force *d* is known shortly as the " suction pressure," and is the net force bringing water into the cell. In the fully turgescent cell its effect is nil, for *c* drives out the product of *b* minus *a*. However, in the less-than-turgescent cell (that is, one suffering from deficiency of water or in the wilting condition) the effect of the wall may be considerable.

If the wall is a very elastic one it contracts, step by step, along with the protoplast, and with a pressure steadily falling in value as the cell progressively loses water. If any water is available to the cell it will enter only slowly because of this continuing pressure of the elastic cell wall. Hence under temporary

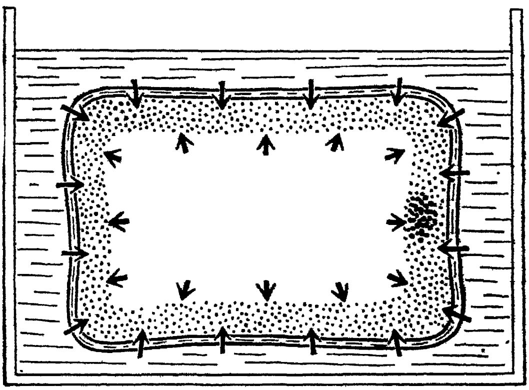


FIG. 118

The forces resident in a cell

drought conditions the net amount of water coming into the cell and remaining there increases only slowly.

On the other hand, if the wall is rigid and not elastic the position is rather different. As before, at full turgescence the wall presses the protoplast with a force equal to that with which the protoplast presses the wall. When the cell loses the least amount of water and the protoplast shrinks in the very slightest, the protoplast will stop pressing the rigid wall completely. When this happens the wall pressure will fall at once to zero value. No water will be pressed out of the cell. In short, in a cell with a rigid wall and less than full turgescence, none of the effect of the force causing water to diffuse in will be cancelled. Such a cell with a rigid wall on slight wilting will tend to hold its water content and recover to turgescence much more quickly. This is of great importance to plants which may be subjected to temporary drought, say on a dry summer afternoon.

Plasmolysis

The elasticity or rigidity of the wall in any particular case can be readily demonstrated. If with an isolated cell the direction of the water gradient is reversed by decreasing the concentration of water molecules outside to less than the concentration inside, exosmosis will occur and the equivalent of wilting will result. Mounting cells in a solution with a concentration of dissolved molecules higher than that of the cell sap has this effect.

When a group of cells possessed of elastic walls is immersed in a solution more concentrated than their sap, the whole unit is first seen to decrease in volume; then the protoplast of the individual cells recede from contact with the walls. As the water progressively diffuses out, each protoplast shrinks further until the vacuole is extinguished, and the cell contents are seen as a ball lying in the centre of each cell. This shrinkage of the protoplast is given the name of plasmolysis.

Measurement of the Osmotic Value of the Cell-sap

An amplification of this technique may be used to measure the osmotic value of the cell-sap solution. When cells are immersed in a solution of just sufficient concentration to cause plasmolysis to start in cells with rigid walls, or wall-shrinkage to set in in

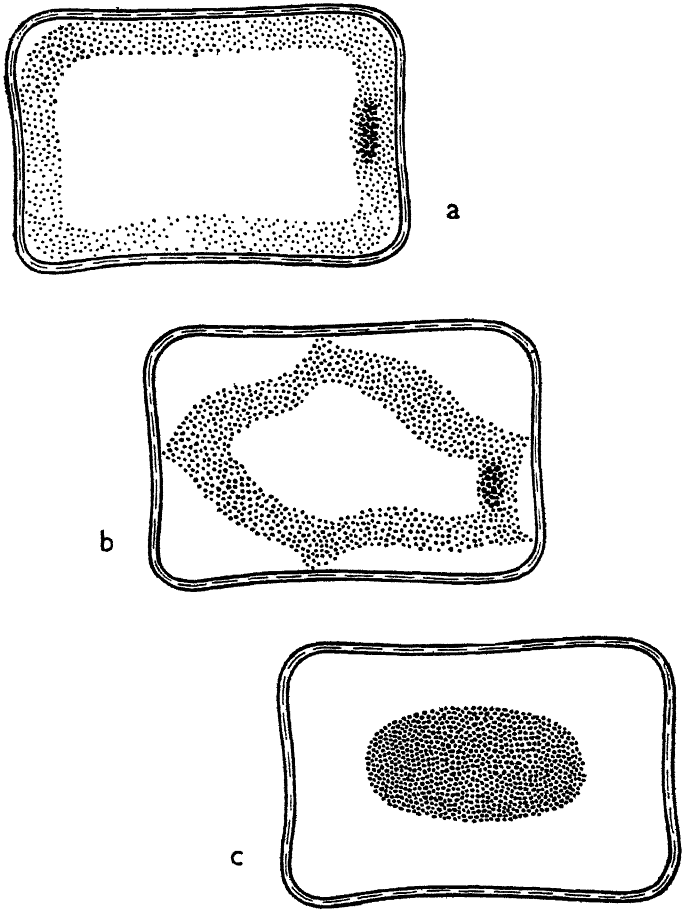


FIG. 119

Plasmolysis

An isolated cell with the water gradient in an outward direction. (*a*) The stage at completion of wall shrinkage—incipient plasmolysis; (*b*) partial plasmolysis; (*c*) total plasmolysis

cells with elastic walls, it is assumed that the solution outside has very nearly the same molecular concentration as that inside. A solution with exactly the same concentration of solvent molecules as the cell-sap is said to be isotonic or isosmotic with it.

There is one aspect of the entry of water into the cell which has not been considered. There are cases where water goes into the cell against the gradient. Mechanically, this is equivalent

to suggesting that water flows uphill. Energy must be expended. The mechanism causing molecules to pass through the semi-permeable protoplast against a gradient is not so well understood in connection with water as it is with solute intake, and further consideration of these cases may be deferred until salt intake has been dealt with.

Cell Posture as affected by Water Intake

Returning to consideration of changes in size or shape (posture) of cells, the special case of the guard-cells of the stomata may be discussed now. It will be remembered that the two cells involved are crescent-shaped and fixed together at their ends. The walls of the guard-cell are thin except on the aspect which faces into the intercellular space between them—the stoma pore. On this face the guard-cell wall is much thicker. When the guard-cells " inflate " with increasing volume the wall towards the ordinary epidermal cell stretches more than the wall adjacent to the pore. Thus as the two cells swell up with incoming water the elastic walls away from the pore stretch, while the rigid walls lining the pore remain unstretched. This increases the curvature of the cell, and it becomes more concave to the pore. This of course makes the pore round as the lips become further apart.

Under drier conditions the reverse process is seen. The guard-cells lose volume and they " deflate." The thin elastic walls contract while the thickened wall remains rigid. In these circumstances the guard-cells tend to become straight, and the lips of the pore approach each other. In short, the degree to which the pore is open depends on the posture of the guard-cells. These cells when swollen up are curved concave to the pore. When not fully turgid they are more linear. These alterations in posture with change in volume are the result of the elastic nature of the guard-cell walls farthest from the pore and the rigidity of the walls adjacent to the pore.

The Grass Stoma

The grass stoma, with its somewhat different construction, behaves in a quite parallel manner. The thin-walled heads of the dumb-bell shaped guard-cells swell easily to carry the middle, narrow, thick-walled portions away from each other, so widening the slit-like pore.

The Cause of Alterations in Guard-cell Volume

There is no controversy as to this aspect of the mechanism. There are different views as to how it is actuated, how the water which increases guard-cell volume is attracted inwards. All the views have common ground in insisting that the presence of chloroplasts in the guard-cells and their absence from all the other cells of the epidermis is highly significant. Because of the presence of these chloroplasts the guard-cells are the only ones in the epidermis capable of changing carbon-dioxide gas and water into sugar when exposed to light.

The older theories regarding guard-cell posture held that in light the guard-cell manufactured soluble sugar. The addition of this lowered the molecular concentration of water in the vacuole, and so upset the water equilibrium between the guard-cells and their neighbours. Because of the gradient so formed water diffused from the epidermal cells into the guard-cells, increasing their volume. The pore opened. As long as light continued, sugar was manufactured. At all times sugar seeped away from the cell, but usually synthesis manufactured more than seeped away. The upper limit of sugar content was not exceeded because when this point was reached an enzyme in the guard-cells commenced to condense the sugar to starch.

In the dark synthesis ceased, movement outwards of sugar continued, hence the sugar content in the guard-cells fell. The starch in the cells was hydrolysed back to sugar, which in turn seeped away. In time the total carbohydrate fell to a level providing osmotic equilibrium with the neighbouring epidermal cells, and the water gradient between all the cells of the epidermis, guard and ordinary, flattened out. The guard-cells then contracted from full turgescence and the pore closed.

Objections to Simple Theory of Guard-cell Movement

There are a number of objections to this simple theory. The first objection is its slowness ; it would operate too slowly to meet the observed facts. A second is that stomata often open in the dark and commonly close in light. A third is that the stoma pore is the path into or out of the tissues through which all gases involved in any function must pass. Respiration demands intake of oyxgen and output of carbon dioxide. Carbohydrate synthesis demands that carbon dioxide move inward and oxygen out. As

regards water it is important that outward movement of water vapour should stop whenever there is danger of loss of water vapour from the leaf tissues going to an extreme. All these gases diffuse through the pore, each on its own gradient, and the degree of opening (posture of the guard-cells) is a major factor in controlling the amount and speed of each simultaneously. The stoma, therefore, must be so actuated as to strike the best balance between all possible demands of all these functions, and when they conflict a compromise must be effected. For example, the stoma must close in light if water-loss is proceeding to such an extent that the leaf may dry out, and it must do this despite the fact that conditions may be ideal for sugar synthesis. Again, the pores must be open on a warm night if respiration is producing so much carbon dioxide that there is danger of its accumulating in the tissues with poisonous effect.

Later Suggestions on the Mechanism affecting Guard-cell Posture

The newer theories of the stomatal mechanism regard the hydrogen concentration of the guard-cell as the " trigger " between prime cause and effect. By variation of the H.I.C. the turgescence of the cells is altered. The acid supplying the active hydrogen ion being carbonic acid (H_2CO_3) formed from the solution of carbon dioxide (CO_2) in water.

Exposure to light, in presence of chlorophyll, converts the acid in the cell to sugar. This reduces the H.I.C. In the dark, as a result of respiration, the carbonic acid content and therefore H.I.C. rises. That these alterations in acidity happen, and that alterations in guard-cell posture follow, is an observed fact.

Theories on how the mechanism operates have not followed the lines of explaining anomalous opening and closing so much as of demonstrating that in the guard-cells the equilibrium of the starch $\rightleftharpoons$ sugar reaction is controlled by H.I.C., which in turn is controlled by H_2CO_3 content, which is controlled by the sugar synthesising mechanism. This explanation is summarized in Fig. 120. In this figure light is omitted as a distinct factor because it is implicit in the term " photosynthesis."

Starting with the central photosynthesis—this in the guard-cells controls their carbon dioxide content, which controls their H.I.C., which controls the amylase activity, which controls the starch$\rightleftharpoons$sugar ratio, which controls turgor, which controls the size

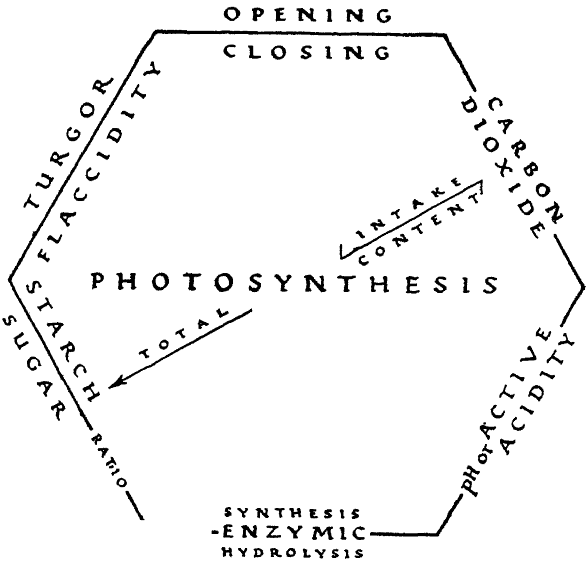


FIG. 120
The mechanism of stomatal movement
(*From J. Small and co-workers, Proc. Roy. Soc. Edin. 1942*)

of the stomatal aperture, which controls the rate of gas exchange and therefore the rate of intake of carbon dioxide for the supply of the general photosynthetic activity of the leaf as a whole.

Sugar content of the guard-cell affecting the osmotic gradient is used in the new as in the older theory, but now the sugar content is seen to be controlled by a much quicker acting mechanism, rising or falling H.I.C. affecting the equilibrium point of the amylase enzyme. This line of thought has not so far explained the opening of the pore in the dark, but it is likely that this will eventuate soon.

Closure, when it occurs, in normal daylight is probably due to water loss from the guard-cell by simple evaporation. The guard-cells are the only cells of the epidermis not protected by cuticle, and hence dry out easily. Shrinkage of guard-cells due to water loss will of course close the pore.

The Water Balance in the Plant

Uncuticularized walls on the outer surface of a plant are not common. Apart from very young leaves emerging from the bud, motor tissue as noted in grass leaves, and the guard-cells, surface

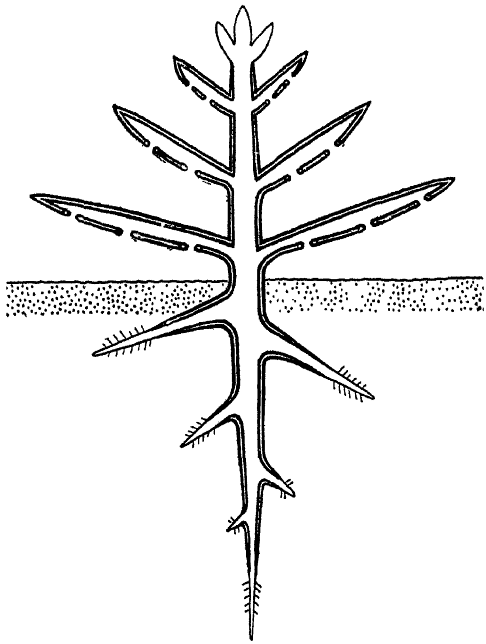


FIG. 121
The whole plant is enclosed in cuticle except for the youngest portion of the shoot, the stomatal guard cells, and the absorbing region of the root

cell walls lacking cuticle are confined to that portion of the root where the root-hairs normally occur.

In short, the whole tissues of the plant, root and shoot, are enclosed within an almost complete envelope of cuticularized epidermis. The degree to which the cuticle retards the diffusion of water molecules depends on its thickness; a thick cuticle is almost completely impermeable to water.

The Region of Water Intake

All the water passing into the normal crop plant must come in through the root hair region. The cells of the piliferous region, whether " blistered " out into root hairs or not, provide the only path of entrance for all molecules, water and otherwise, coming from the soil.

The walls of the cells of this root hair region are of unmodified highly hydrated cellulose. Furthermore the cellulose is most

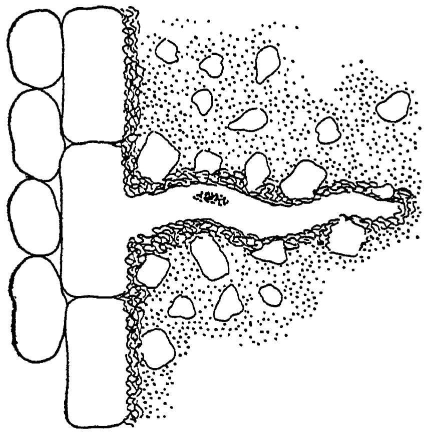


FIG. 122
The root hair in contact with the soil
Two cells of the piliferous layer have not formed hairs

dispersed on the external aspect; that is, where the walls make contact with the soil. Indeed, the walls of the root hair may be imagined as being comparatively dense (gel state) towards the vacuole, and gradually approaching a sol where they contact the soil water and soil colloids.

The Water Continuum between Soil and Plant

There is, then, continuity between the water of the water-dispersed colloidal wall and the water of the water-dispersed soil colloid. Not only so, but the wall of the hair being so thinly gelatinous, tends to partially occlude such particles of the soil as it may press against it in its development. As will be seen in a moment, this ensures that the water of the colloidal wall is continuous with the soil water. Water, then, is continuous from the soil through the walls of the cells of the piliferous layer. Water is the continuum between the cells of the plant and its environment.

The water of the soil may be regarded as held in four different ways. There is the water of crystallization of chemical compounds in the soil. This is of no use to the plant. There is water as the dispersion medium of the colloidal fraction of the soil. Water held by capillary attraction on the surface of inorganic soil particles makes up a big proportion of the total soil moisture. Finally, in the water-logged state there is free water occupying

the pore spaces of the soil. This last, by displacing air, is in the main deleterious to plants. Of all the water in the soil, only a portion of the colloidally held fraction and a portion of the capillary held quota is of use to the plant.

The Entry of Water into the Root

The mechanism by which water enters the plant may now be described. The molecules of water diffuse from the soil along the colloidal walls of the root hair to the wall of the first cell of the cortex, and then along the walls of the deeper tissues to the endodermis. At the endodermis, if the suberized thickening has developed as is usual on the radial walls of the cells there, this movement in the colloidal walls is interrupted.

While this is going on, provided the osmotic value of the cell-sap of the root hair is higher than that of the soil—that is, provided there is a water gradient inward—water passes by osmosis into the hair. This intake of water into the vacuole of the root hair lowers the osmotic value of the sap of that cell, and a water gradient is thus constituted between it and its neighbour in the cortex. Water then passes by osmosis from the root hair to the first cell of the cortex. This process goes on from cell to cell inwards, giving a compound gradient from the soil solution to the stele. Here the water enters the xylem, and if not quickly sucked away a pressure of water is set up in the vessels.

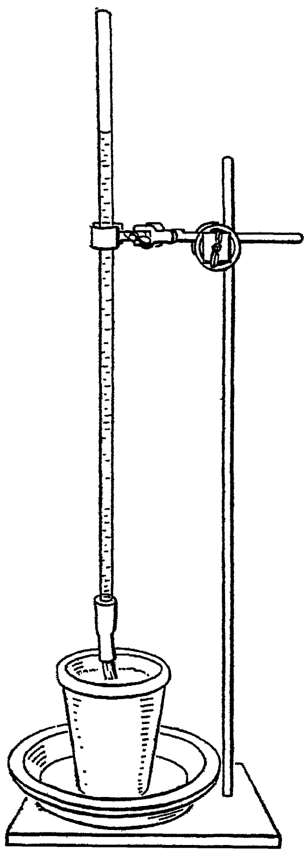
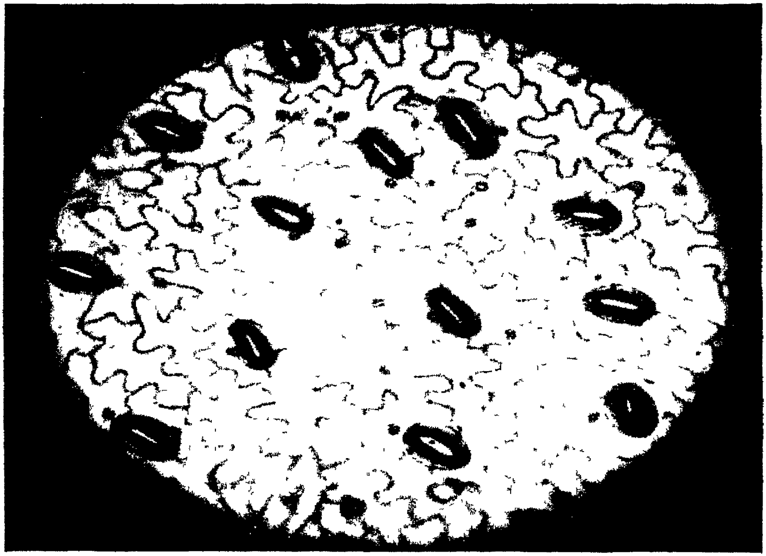


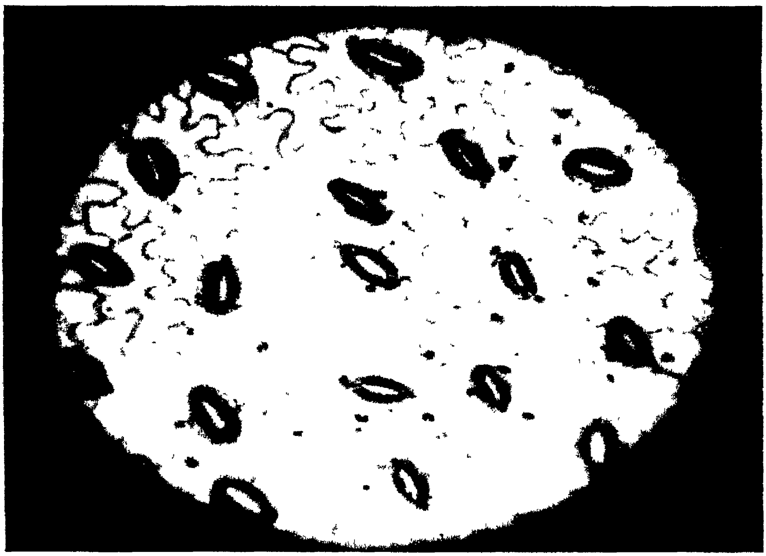
FIG. 123
Root pressure
The rooted stump of a cut-off stem forces water upward in the glass tube

The Rate of Entry of Water into a Root

If the solute strength of the soil solution be unduly raised, as by the addition of heavy dressing of a soluble manure,

PLATE 55 ONTOGENETIC RESPONSE IN A MESOPHYTE





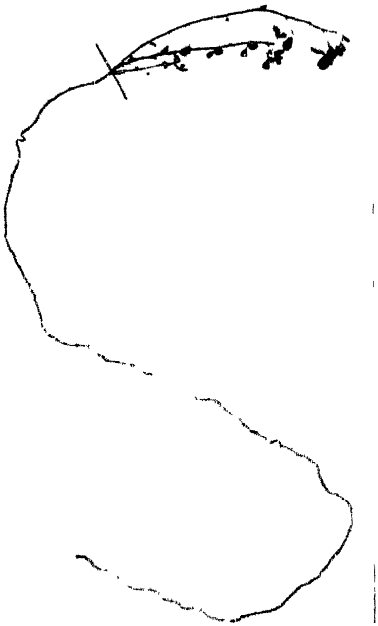
LOWER EPIDERMIS OF BROAD BEAN

Above Grown under humid conditions (13 stomata in microscope field)

Below Same grown in dry air (19 stomata in microscope field). The magnification of both preparations is identical

AN EPHEMERAL PLANT: SUBTERRANEAN CLOVER

This plant normally straggles along the ground rarely producing adventitious roots. When the seeds ripen the stalks which bear them bend and place them in the soil



A DROUGHT-EXPLOITING PLANT: LUCERNE

This young plant has developed its enormous tap-root but very little top growth. (A portion of tap-root was lost during extraction)

the water will diffuse out of the root and not inwards, and plasmolysis of the cells may result.

Soil temperature is important. Within what may be regarded as a congenial range for most plants, say between 10° and 15° C., the rate rapidly increases with increase of temperature, and obeys the Van't Hoff rule, which says that the increase in rate of function for every rise of 10° C. is a constant. This constant is symbolized by Q_{10}. The value of the constant for water absorption by a root at normal levels of temperature is about 1·3. The rule does not apply to water intake by the root at abnormally low or high temperatures, because the living protoplasts are then adversely affected.

The rate of absorption by a plant is always higher than would be possible in a purely physical diffusion system under the same conditions, and it does not obey the same rules. For example, a decrease in temperature from, say, 20° to 0° centigrade depresses the rate of water intake by about 25 per cent., while over the same depression of temperature an osmometer would show only a small fall in rate. The living cells have a vital part to play in the process. These effects may be due to changes in permeability or of viscosity of the protoplasm, but it may be that they are connected with the expenditure of energy in intake, a phenomenon now better understood in connection with solute intake.

The acidity of the soil solution, too, affects the rate of water intake, and it is fairly well established that an acid state about the root reduces the rate at which water enters.

As has been noted already, increase in the osmotic strength of the soil solution following an application of a soluble manure, reduces the rate of water intake. There is evidence, however, that if such an increase in the salt content of the soil solution is not so extreme as to cause death of the cells from wilting, the plant, given time, will accommodate itself to the higher solute concentration. This may be due to the manurial salt diffusing into the root cells and raising the salt content of the sap. Many species of plant have developed an inherent ability to live in soil of a high salt content. These inhabitants of salt marshes and similar situations are known as Halophytes.

Forces which Resist Water Intake

In the normal case, where the strength of the soil solution is less than that of the vacuole sap, and the water gradient is inwards,

there are forces outside the plant resisting the intake of water into the root. There is the concentration of the solutes dissolved in the soil water. There is the water-binding power of the soil colloids, and there is the attraction the surfaces of the inorganic particles of the soil have, like glass, for water. If there is sufficient water present to satisfy fully all these water-retaining forces, then the resistance is slight or nil. As the soil dries, however, the colloids present become less fully hydrated, and at the same time the layer of water around each soil particle becomes thinner. Thus as the plant takes water away from the soil the remnant left there is more tenaciously held. Hence in a drying soil the portion of water still held by each of its several fractions is retained with increasing power. Under these circumstances of falling soil-water content the pulling power of the plant increases too, but if the process goes on until the forces of the soil equal or exceed the forces of the root, the whole of the tissues of the plant will begin to suffer from restriction of water supply. The

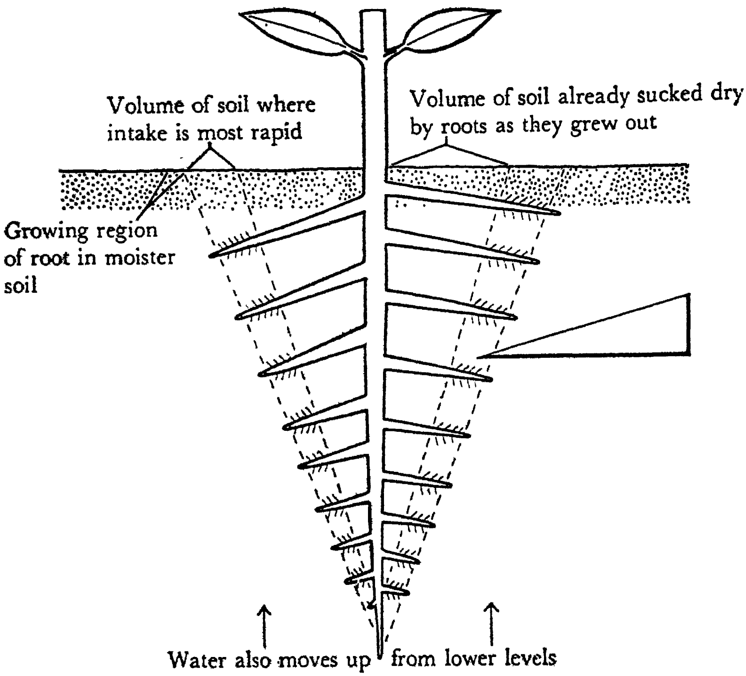


FIG. 124

Diagram showing plant soil relationship with reference to water supply

individual cells will become less than fully turgid. They become flaccid, and the organs they form, such as leaves and stem, are said to wilt.

Movement of Water in the Soil caused by the Plant's Activity

A soil-water deficit caused by the plant's intake in the early stages is localized round the immediate neighbourhood of the root. This causes a gradient to form in the soil, with its low point at the root and high level out in the soil mass. Water then moves towards the root from the more remote regions of the soil. This movement may be a very fine-scale mass flow over the surfaces of the inorganic particles, or a movement of the dispersion medium of the soil colloids may be involved. No matter which (possibly both) is involved, the move is on a diffusional pattern, *i.e.* from a region where there is more to a region where there is less. These movements of water through the soil are comparatively slow, and they may not be able to keep up with the plant's requirements quickly enough, so that unless there is a reduction of demand the plant will wilt. If the giving off of water from the shoot is efficiently controlled and reduced quickly and sufficiently, the demand at the root will so abate that the supply moving in through the soil will equal it, and such wilting as occurs will be merely temporary.

Wilting Point: Wilting Coefficient

When plants are grown in pots the volume of soil about the roots is comparatively small. When wilting occurs in these circumstances there is no mass of soil, and therefore no distant reserve of soil-water to move in. If no water is added to the pot when the plant wilts the plant will not regain its turgidity, and wilting is permanent. It is necessary to differentiate between temporary and permanent wilting. In temporary wilting the plant/soil system, if given time, draws on "distant reserves" and adjusts itself so that the plant recovers its turgidity. In permanent wilting the plant/soil system has no reserves available, and the plant recovers only if water is added from an external source.

By means of pot experiments it is possible to determine accurately the percentage of water still held by the soil at the moment when the plant just fails to draw water from it, and shows its first signs of wilting. In short, it is possible to determine

the point at which the forces retaining water in the soil just equal the pull of the plant. The water content of the soil (by weight) at the wilting point, expressed as a percentage of the total weight of the soil in the pot, is called the *wilting percentage*, or the *wilting coefficient*.

The magnitude of the coefficient is conditioned broadly by the texture of the soil, or the sum of the values of all the forces in the soil acting in the retention of water.

As regards any particular plant, neither its age nor history affects the value of the wilting coefficient. Exposure to partial drought when young will not " educate " it into increased pulling power. The mechanism controlling water-loss from the shoot can be developed during the lifetime of the individual, but not the power of intake.

Different *kinds* of plants, as a result of evolution over long periods, have developed increased powers of water absorption. Also different *kinds* of plants have very different powers of survival while in the wilted condition. It is to these two evolutionary responses and to other responses in the shoot that the introducer of new plants looks for drought-resistant kinds.

BOOKS FOR FURTHER READING

DAWSON and DANELLI. *The Permeability of Natural Membranes* (Cambridge University Press, 1943)

KRAMER, P. J. " Absorption of Water by Plants " (*The Botanical Review*, 11 (6), 1945)

MEYER, B. S. " The Water Relations of Plant Cells " (*The Botanical Review*, 4 (10), 1938)

CHAPTER XI

THE OUTPUT OF WATER BY THE PLANT

IT will be necessary to return in a later section to a further consideration of water intake at the root, but in the meantime attention may be turned to a consideration of the fate of the water absorbed. The description of water intake at the root reached the point where the water entered the xylem. Once within the tube-like vessels the water passes easily by mass flow to the furthest and finest ramifications of the veins.

Under normal conditions, more water arrives at these venules than is used in the formation of foodstuffs or is required for full hydration of the tissues. The greater proportion of the intake now has to be put out of the plant. The necessity for the intake and transport of this enormous amount of water arises from the fact that it is the carrier of all salts required by the plant in making the more complex foodstuffs. The fast transport of the watery solutions from the root is important for carrying up the solutes ; diffusion of the solute molecules all the way up through the plant would be too slow to satisfy requirements. The solutions, too, must not be over-concentrated, else difficulties of osmosis in the intake region or in the tissues of the stem will arise.

In the shoot system this surplus water must be got rid of as vapour, leaving the soluble salts behind. In short, the solution distributed to the synthesising parts must be evaporated down. Osmotic difficulties do not arise in the shoot as a result of this concentration, because the salts are at once " built into " foodstuff molecules and taken out of the active diffusional system.

The process of evaporation requires to be under control, else it might go too far and the tissues dry out in droughty weather.

The Tissues involved in the Output of Water

For a proper understanding of how this output is accomplished a recapitulation of the anatomy of the typical leaf is necessary. It was shown in pages 38 and 60 that the air spaces of the whole plant (including those of the leaf) form a continuous intercommunicating network. The network communicates with the

outer air only through the stoma pores. The stoma pore is an intercellular space in the cuticularized epidermis.

The cuticle is regarded here as being totally impermeable to water either as liquid or vapour. This is not strictly so, for the degree to which it is permeable to water molecules is roughly proportional to its thickness. Any diffusion there may be through the cuticle is not subject to control. Apart from some little movement through the cuticle, the stoma pore must be regarded as the only channel for gas-exchange between the internal atmosphere in the intercellular spaces and the external atmosphere.

The Efficiency of the Stoma Pore

The pores of the stoma when fully open are very small, each of the order of 0·0000908 sq. mm. area. The total area of the whole of the pores of a normal leaf of sunflower amounts to only 1 per cent. to 3 per cent. of the total area of the leaf. Despite this they are responsible for practically all the gas exchange between the inside and outside of the plant. When these small pores are open the amount of any gas passed out or in is as much as if the cuticle were not there and the mesophyll cells were completely exposed to the air. When the pores close, gas exchange between the two atmospheres inside and outside the plant practically ceases.

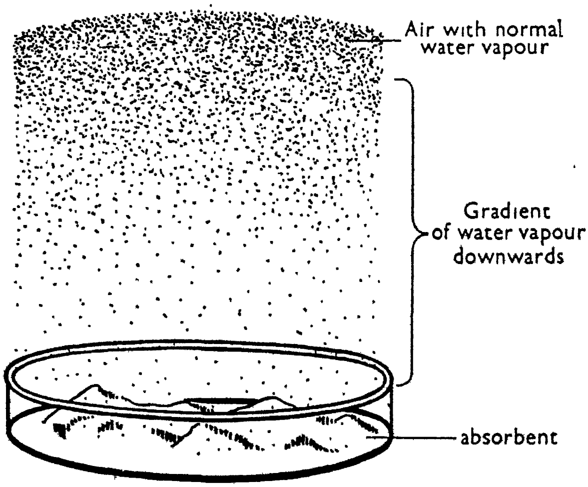


Fig. 125
Diffusion gradient of water vapour above a dish of absorbent (columnar diffusion field)

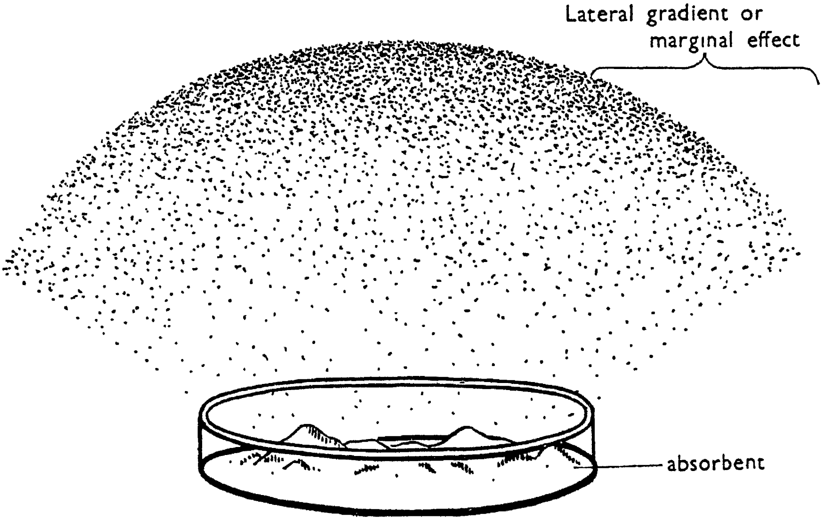


Fig. 126
Fig. 125 corrected to show lateral gradient forming a fan-shaped field (marginal effect)

The explanation of why so few pores of such small aperture can provide such an efficient channel is simple.

Consider a round dish or saucer and place in it a layer of some water vapour absorbent such as concentrated sulphuric acid. At once the absorbent will take up from the air the water vapour molecules at its surface. This will constitute a small local gradient, and before very long there will be a columnar volume of air above the dish in which there is a gradient of water vapour downwards as shown in Fig. 125. The picture of a column is not accurate, however, for all round the column of air above the dish there will be a lateral gradient. Hence instead of a column of air being denuded of its water vapour there will be an area "fanning out" in all directions—see Fig. 126. This is diffusion at a margin.

If the diameter of the dish be progressively reduced the margins of the dish approach. Thus by contraction a dish size is arrived

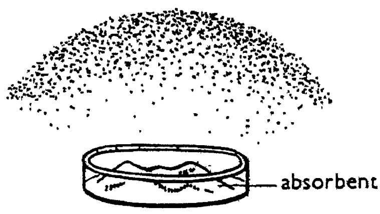


Fig. 127
In a very small dish a greater proportion of the total diffusion is lateral (marginal effect intensified)

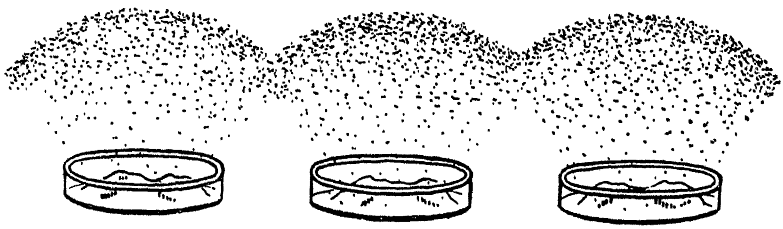


FIG. 128
A number of small dishes with the lateral gradients overlapping

at which provides the maximum marginal effect—see Fig. 127. If now a number of such dishes be envisaged, and these brought near to each other, a spacing between them is possible which just causes the outer edges of the diffusion fields to approach each other. Thus a set of dishes of absorbent each exposing an ideal area, and distributed over a table in an ideal spacing will absorb as much as if the whole table surface was covered with absorbent—see Fig. 128.

If the table were wholly covered with absorbent but separated from the air by a metal plate, and this plate had perforations drilled in it of the ideal size and at the ideal spacing, gas would pass down to the table surface as if no plate were interposed (Fig. 129). The cuticle of the leaf is merely such a perforate plate or perforate septum interposed between the two atmospheres. The stoma pores are very near to the ideal size, and are

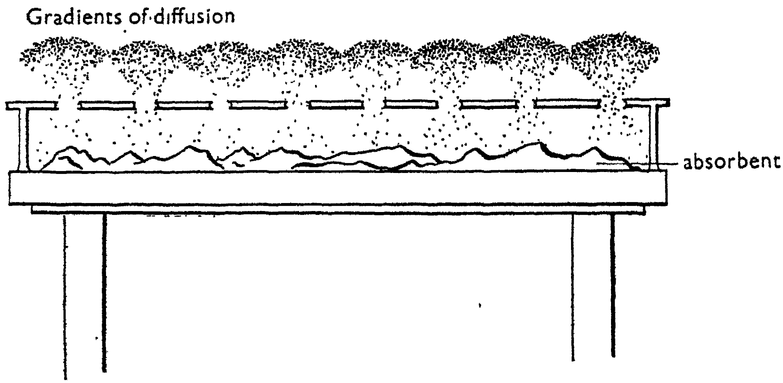


FIG. 129
The gradients when the absorbent is separated from the atmosphere by a sheet pierced with holes (a perforate septum)
The perforations are shown as of an "ideal" size and spaced at an ideal distance

distributed on the leaf surface at about the ideal spacing. The cuticularized epidermis behaves as the body of the metal plate in the example, and the stoma pores are the perforations. The efficiency of the pore is thus explained on the well-understood and proven theory of diffusion through a perforate septum.

Gas Diffusion Gradients through the Stoma Pore

If the internal atmosphere of the leaf is more humid than the outer air, then an outward gradient of water vapour exists. If the leaf is consuming oxygen in respiration there will be a gradient of oxygen inwards and of carbon dioxide outwards. If it is consuming carbon dioxide in synthesis and giving off oxygen, these gases will pass through the pores. Each of these gases passes in or out on its *own* gradient independently of any other.

TRANSPIRATION

Transpiration is the controlled giving off of water vapour from the shoot of a plant, and takes place through the stoma pores.

In considering stomatal transpiration it will be advisable to commence with a state of equilibrium. Suppose the cells of a leaf are fully turgid and the external atmosphere is fully charged with water vapour, or in other words, it is saturated and not capable of holding any more, it is at the dew-point. There will be no gradient of water vapour through the pore (which may be imagined as open), and hence no diffusion (transpiration). In this condition the cells of the tissues will be fully charged with water and incapable of retaining any more. The colloidal system of the tissues too will be fully hydrated. In this condition the fully hydrated cell walls will hold water molecules no more tenaciously than a free water surface would.

Now let the water-holding power of the external atmosphere be increased as by a rise in temperature or by the flowing in of a current of dry air. This causes a difference in water vapour concentration between the internal atmosphere, fully charged with water molecules, and the now drier air outside. Water molecules will now diffuse through the open pore outwards down the gradient so formed. The internal atmosphere of the intercellular spaces now becomes less than fully saturated, and water molecules fly off the saturated walls which are adjacent

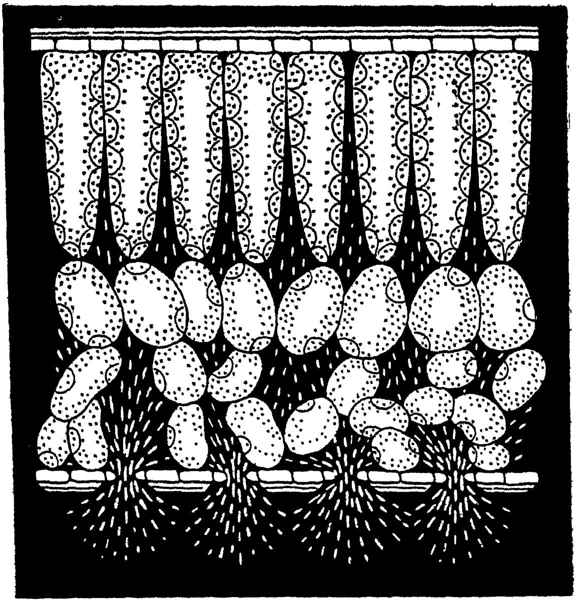


FIG. 130

V.S. of leaf to show gradient of diffusion of water vapour when outer air is drier than the air of the intercellular spaces

to the intercellular spaces. The colloidal walls become less than fully hydrated, and are now capable of exerting a "pull" on a more hydrated region of the tissue. The walls recoup themselves from walls not bordering the spaces, and so the whole mass of the colloids in the leaf tissue is less than fully hydrated and exerts an attraction for water.

The water of the cell-sap will then be drawn upon, the cells will become less than turgid, and an osmotic pull for water created.

The whole of the leaf tissue now operates both as an osmometer and as a partially dehydrated colloid mass. The only source of water available to meet this dual demand is the liquid in the xylem vessels of the veins. The watery dispersion medium of the colloidal walls of the vessels and cells forms a continuum between the sap of the cells and the mass of water in the xylem, so that the pull set up in the drying tissues is readily carried back or transmitted from cell to cell, and so to the liquid in the vessels.

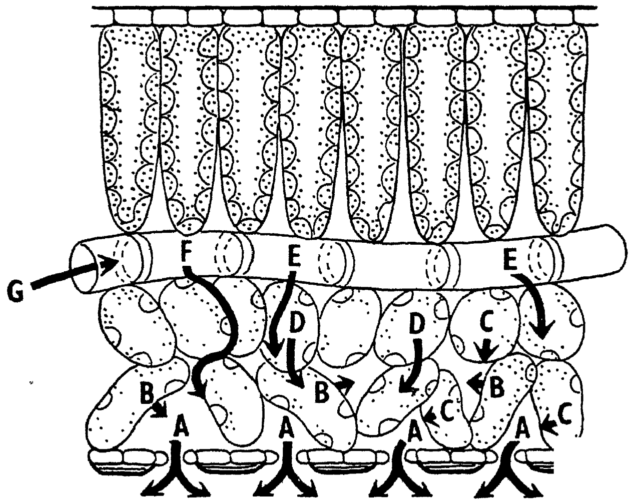


FIG. 131

V.S. of leaf to show the various gradients involved in the different steps in transpiration

(*a*) Water vapour diffusing as a gas from intercellular spaces through stoma pore to outer air

(*b*) Water molecules leaving dispersion medium of colloidal wall and protoplast

(*c*) Water molecules leaving cell sap to become part of dispersion medium of cell colloids

(*d*) Water moving by osmosis from cell to cell

(*e*) Water diffusing from xylem vessel to cell sap by osmosis

(*f*) Water moving from vessel into and along the intermicellar spaces of the cell colloids (a form of sub-microscopic mass flow)

(*g*) Liquid water being pulled through the vessel by virtue of molecular cohesion (mass flow)

The picture is one of a series of individual gradients running back step by step from the dry external atmosphere through the stoma pore to the intercellular spaces to the cells and walls and ending on the liquid water of the vein. Normally the whole progression from the vein to the air is so smooth, and the different components in such perfect balance, that the whole may be regarded as one composite gradient.

In the xylem vessels the watery solution is, of course, in the liquid form and capable of moving as such. As it passes out of the xylem through the intermicellar spaces of the wall the attraction between molecules permits each to "drag" the one behind up into

the place it has vacated. The result is that, due to molecular attraction or cohesion, the threads of water in the vessels are pulled upwards. These slip along inside the vessel very much like the wire inside a flexible brake cable. The threads, again due to molecular cohesion, are very strong and elastic, as may easily be seen in the case of the thread-like contents of a very fine capillary tube filled with water.

Thus the deficit of water vapour in the outer air causes a deficit in the shoot tissues which, by recouping itself from the liquid in the vessels, exerts a pull on the contents of vessels, and the dilute solution is drawn towards the area of shortage from any area of comparative plenitude. The current through the vessels so set up is the transpiration stream.

The Transpiration Stream

The direction taken by the transpiration stream is normally from the point of intake in the root up into the shoot, that is, from below upwards. By manipulative methods, however, the threads of water may be made to move in any direction. The only rule is that they always flow from an area of comparative water plenitude to an area of comparative scarcity. For example, if an actively transpiring plant has the tip of one of its leaves placed below the level of a dilute aqueous solution of a dye such as eosin, and the submerged tip cut off, it will be seen that the dye "jumps" into the vessels of the severed veins.

The water in the vein, being under some tension from transpiration, behaves when cut like a piece of elastic and contracts back. The attraction between the liquid water in the vein and the dye solution pulls the coloured liquid inwards. If the plant as a whole continues to transpire and the cut leaf remains with the wounded tip below the surface of the dye solution, the coloration will be seen to travel back down the mid-rib, into the stem, and eventually to all parts of the plant which are losing water. If a leaf near the apex of the shoot had been selected for the experiment, then the dye solution will travel downwards. The extent of the initial "jump-in" will depend on how far the supply from the root was lagging behind the rate of transpiration at the moment of cutting. The rate at which the dye subsequently travels back will depend on the same ratio.

Factors affecting Transpiration

(1) *Relative Humidity of the Air.*—It is obvious that the relative humidity of the air surrounding the plant is the factor most profoundly affecting the rate of water loss.

(2) *Temperature.*—Temperature does affect transpiration. A rise in temperature increases and a fall in temperature decreases the amount of vapour passed out. This is largely due to the change in relative humidity altering the steepness of the diffusion gradient, for warmer air can hold more water vapour than cold air.

Increase in temperature causes a volume of gas to expand, and following such a rise part of the gas confined in the intercellular spaces may press out through the pore. This is temporary and negligible, and applies to all gases, not to water vapour only.

(3) *Wind.*—A condition of somewhat the same class but of greater practical importance is set up by winds which cause the plant to sway to and fro. Swaying causes the plant stem to become convex to the side the wind is coming from, and concave to the direction it is going. The tough inextensible tissues of the

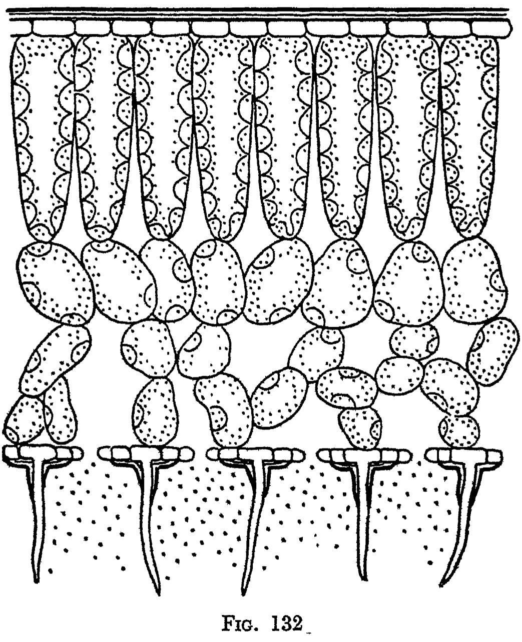


FIG. 132

Hair on the leaf traps water molecules and prevents air currents carrying them off—the gradient " backs-up "

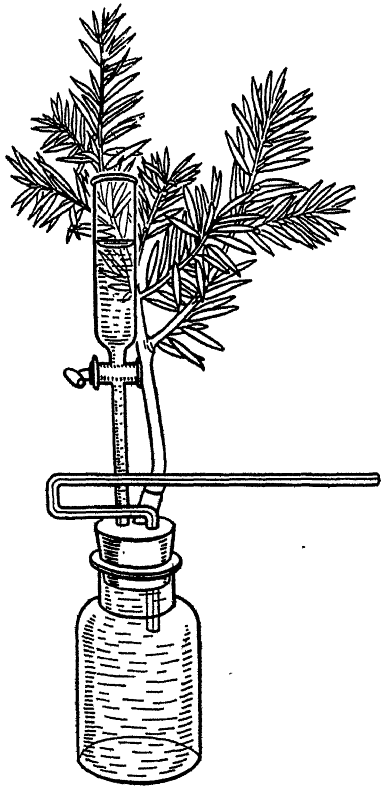


FIG. 133
Farmer's Potometer
As the branch sucks water from the bottle the thread of water in the capillary tube is drawn back. Opening the stop-cock on the thistle funnel refills the capillary and readings may be repeated. The rate of transpiration may be calculated

convex side will press laterally inwards towards the centre of the axis, so compressing the tissues and reducing the volume of the air spaces. On the concave side the opposite will occur. By alternate sways in different directions a bellows effect will be produced, mechanically pressing air out or sucking it in through the stoma pores.

Air currents have another and more potent action on transpiration rate. If the incoming air current (even quite gentle) is not fully saturated with water vapour, then it is capable of taking up more moisture. As it passes across the surface of the leaf it picks up such water molecules as may be there. Thus water vapour molecules issuing from the pore or coming through a thin cuticle have not to await the slow process of diffusion for distribution to a distance, but are carried away at once. The gradient of diffusion at its external terminal is kept as low as the humidity of the air current permits. This action of the wind leads

to death of young leaves, and they are said to be burnt or scorched by the wind.

(4) *The Nature of the Shoot Surface.*—A number of plant variations, in addition to production of a thick cuticle, have developed in evolution which counter the effect of wind. The best example of these is hair produced on the surface. The hairs "entangle" the water molecules which issue from the stoma pore. They ensure the maintenance of a nearly static layer of water-vapour molecules on the leaf surface.

Wax on the surface, too, is regarded sometimes as protection against wind, but the function of this type of covering is rather to reinforce cuticular resistance to transpiration while permitting fairly free movement of carbon dioxide gas. Wax repels water molecules while being comparatively easily permeable to carbon dioxide molecules.

(5) *Light.*—Light is believed to expedite molecular movement and so promote diffusion. It chiefly affects the rate of transpiration, however, through the mechanism of the guard-cells increasing or decreasing the pore dimensions.

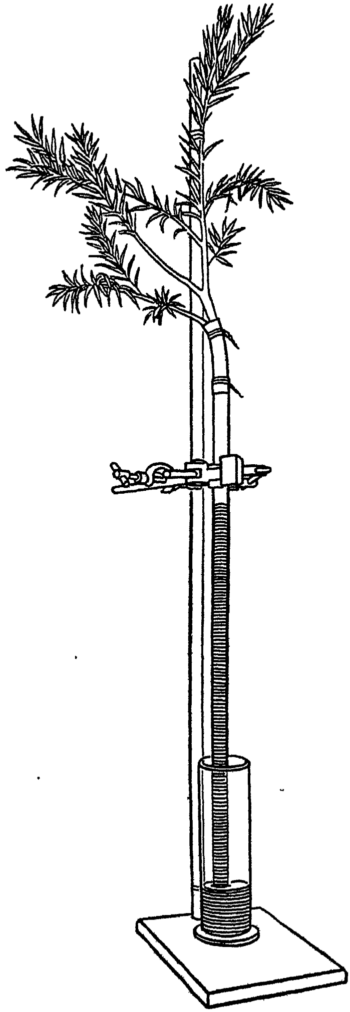


FIG. 134
The power of the transpiration pull. As the branch transpires the water in the tube is pulled up, and pulls behind it the mercury from the reservoir

(6) *The "Vital" Factor.*—It should be said at this point that the process of transpiration is more than a mere evaporation mechanism. For example, it has been shown that a plant can continue to lose water into an atmosphere saturated with water vapour. It is thought that in this case the output of water from the shoot, like its intake at the root, is primarily diffusional in

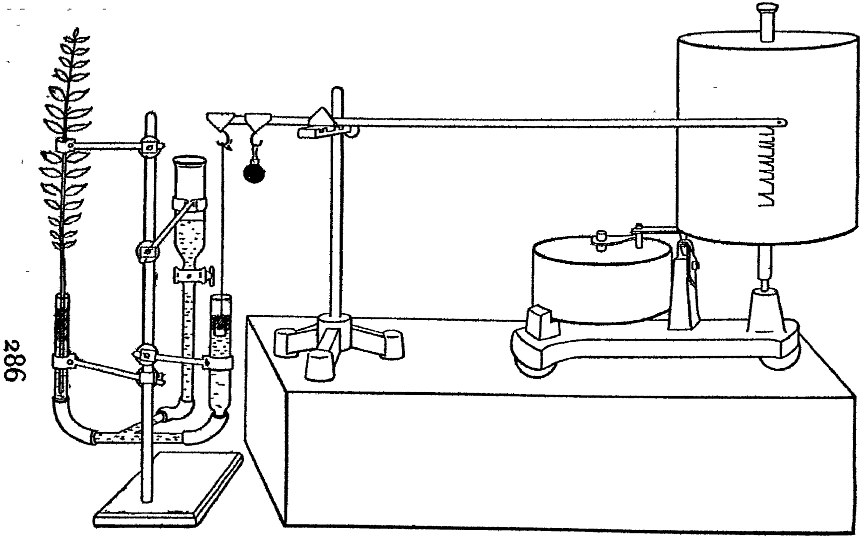


FIG. 135

A recording transpirometer

The branch sucks water, the float falls, and the pin on the lever traces a line. The clock moves the drum on its axis so that transverse lines appear on the drum marking the passage of time. Fig. 136 shows the actual trace made on the drum

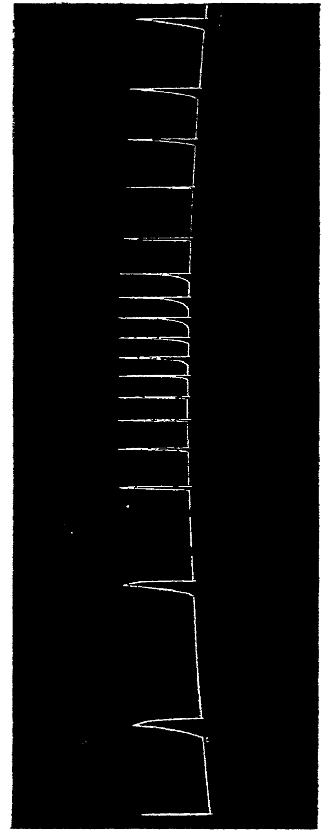


FIG. 136

Trace made by the recording transpirometer

character, but that in addition the mechanism may be assisted by a "vital force" resident in the living protoplasm and using energy derived from food.

Measurement of Transpiration

There are a number of methods for estimating the rate of transpiration and the total amount of water transpired. A pot plant may have the pot and soil surface totally enclosed in a shell impermeable to water. If the whole is then weighed periodically fall in the weight may be ascribed to the water passed out through the shoot.

A branch may be inserted in a potometer, as is shown in Fig. 133.

Potometers measure the amount of water taken in by the plant, and not necessarily the amount given off. They take no account of the water "built into" the food molecules. It has been shown that a shoot cut off from its roots and the cut base inserted in water absorbs just about as much fluid as it did originally through the intact roots.

The amount of water transpired by a branch can also be estimated by the use of a recording transpirometer. In this apparatus the end of the cut branch is inserted in one limb of U-tube which is filled with water. As the branch absorbs water the level of the water in the U-tube falls. As the float in the other limb of the U-tube falls the movement is recorded on a drum of smoked paper. The actual amount of water transpired can be arrived at by simple calculation (see Figs. 135, 136).

Another method consists of measuring the amount of water vapour exhaled by the plant and collected on an absorptive, such as a weighed quantity of calcium chloride.

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CHAPTER XII

ADJUSTMENTS OF THE PLANT TO DIFFICULT WATER CONDITIONS

THE reaction of each kind of plant to different water conditions may be regarded from two different aspects. On the one hand there is the reaction of the individual plant during its own lifetime. This is called the *ontogenetic response*. On the other hand there is the reaction over a long evolutionary history of the race to which the plant belongs, called the *phylogenetic response*. The racial responses fall naturally into three main groups or classes. Firstly, there are those races, etc., which have become adjusted to life in liquid water, the hydrophytes ; secondly, those plants adjusted to areas where water is scarce, the xerophytes. Between these two extremes there are the plants of the "middle way," the mesophytes.

The agriculturist is little concerned with the hydrophyte ; it is only in very special cases that such plants are "cultivated." It is the mesophytes and xerophytes that matter.

The mesophytes, being suited to "middle of the way" conditions, usually have a wide tolerance to fluctuations in the water conditions of their immediate environment. Indeed, it is a general rule applying to adaptation to any factor of the environment that plants not modified to the extent of extreme specialization can exist tolerably well under fairly wide variations of the factor in question.

THE ONTOGENETIC RESPONSE IN MESOPHYTES

Consider first the reaction seen in a mesophytic plant when subjected to difficult water conditions during its lifetime. This most usually arises with the onset of hot, dry weather in summer after a period of "easy" water conditions in spring. Soil water content then falls and the air becomes dry. Intake becomes more difficult and transpiration increases. The shoot of the mesophyte is the part which reacts most quickly. Evidence of the response should be looked for, not in the old leaves, but in those which develop after the commencement of the water

difficulty. The response at first sight seems paradoxical. In a given area of a new leaf the number of veins (particularly the fine branches) and the number of stomata are increased. In short, the mechanism of stomatal (controlled) transpiration and conduction are enlarged.

On the other hand, the thickness of the cuticle is increased. Density of hairs or wax, if either occurs, is increased. The cells of the epidermis are reduced in size. The palisade parenchyma is better developed, while the spongy tissues become more dense with fewer intercellular spaces. The changes in the mesophyll as a whole provide more cells, and therefore more chloroplasts, per unit area of leaf surface. These modifications mean that uncontrolled (cuticular) transpiration is reduced, and the control exercised by the stomata gains in efficiency, while the leaf as a whole is rendered a better light trap.

To sum up, it may be said that a leaf of a mesophytic plant developed under difficult water conditions produces a structure modified in such a way as to ensure increased stomatal transpiration, decreased cuticular water loss, along with improved efficiency in food synthesis.

Why these changes increase the chances of the plant's survival and success may be explained.

Effect of Increased Venation and Increased Stomata

The first point to make clear is that movement of water in a vein is quick. Movement in a vessel is a mass flow, and large quantities can be carried over long distances in a very short time. Movement from cell to cell in the tissues of the mesophyll is by diffusion. Diffusion is a slow process. Unless the gradient is very steep and the distance short, no great amount can be moved quickly. Therefore the closer a cell in the leaf tissue is to a vein the easier and more assured is its water supply. Increasing the number of veins per unit of area reduces the distance between a vein and the cell farthest from it. Increased density of veins shortens the length of the path which the water molecules must traverse by diffusion in getting to the farthest out cell.

Where a vein traverses the mesophyll the intercellular spaces are considerably reduced. Thus the cells of the mesophyll, lying within the islets of tissue between the veins, form an almost isolated group, and each of these must have a stoma pore, or else they

will have only a restricted path for gas-exchange. Increased venation in the leaf, therefore, demands an increase in the number of stomata. This increases the ability of the leaf for gas-exchange generally, not just transpiration. Put briefly, it may be said that increased facilities for water conduction, shortening of the diffusional path, increase in stomatal number, all lead to increased transpiration while the pores are open. It is to be noted in passing that the increased facilities for gas-exchange permit the leaf to produce more food in given time so long as the pores are open.

Within an islet (inter-vein area) the stoma occupies a central position. This means that the guard-cells are the cells farthest from a vein. The guard-cells are therefore the first to be subjected to deficiency of water supply in a leaf where water output is becoming faster than supply from the root. As soon as this deficiency becomes critical the guard-cells lose volume. They become semi-flaccid, and the pore closes. Once the pore closes all transpiration ceases, for the thickened cuticle prevents loss from the general surface. In a mesophyte adapted in this manner to difficult water conditions transpiration is actually increased during any period when the water situation is temporarily easy, but it is efficiently stopped when difficulty arises.

The Phylogenetic Response

The adjustments which have been effected in races of plants long resident in (indigenous to) arid or semi-arid habitats will now be discussed.

Many of these "responses" are of first-class agricultural importance, and may be classified according to the particular climatic type they are attuned to.

The Drought Evader, or Ephemeral Plant

For example, there is the response shown by a large number of plants to summer drought and winter rainfall. Such conditions occur typically in the Mediterranean area. They are also seen in the land areas to the westward of all continents between 20° and 40° latitude both north and south of the equator. This seasonal alternation is often referred to as the Mediterranean climate.

The extent to which this typical climatic cycle occurs in a continent is considerably modified by such factors as the existence

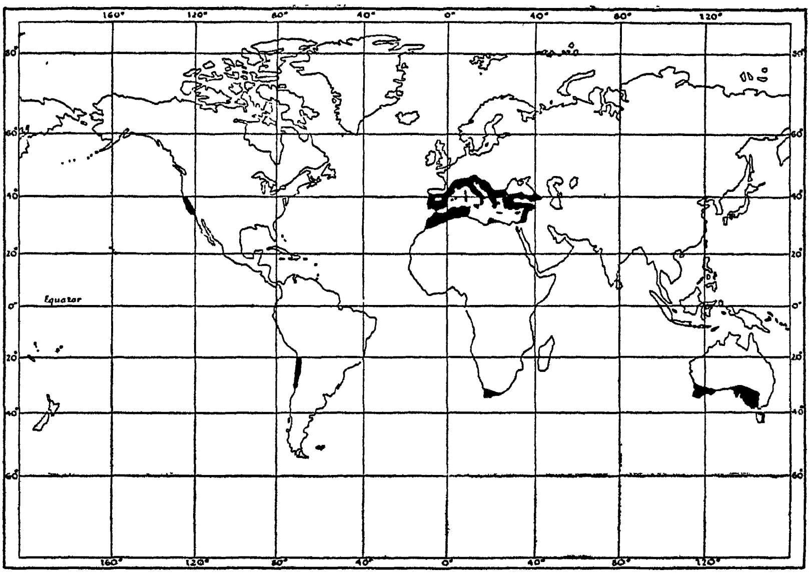

FIG. 137

Map showing regions of Mediterranean climate

of mountain ranges, marine currents, and other more or less local conditions.

In the Northern Hemisphere a belt of country under this climate extends from Turkestan westwards, including Palestine, the coastal regions of the Mediterranean, the north-west coast of Africa, and parts of Spain and Portugal. In America this climatic type appears between the 20° and 40° bounds of latitude westwards from the Cascade and Sierra Nevada mountains to the coast. In the Southern Hemisphere there is a narrow strip in South America between the Andes and the coast. In South Africa the west and south coastal belts are subject to summer drought and winter rain. The same Mediterranean type climates extend through West Australia eastwards as far as Adelaide in South Australia.

How the Ephemeral Plant Functions

The plant of significance to agriculture and attuned to this climate of winter rain and summer drought when other factors such as temperatures permit, is the ephemeral or " drought evader type." A plant of this type germinates from seed in the soil with the onset

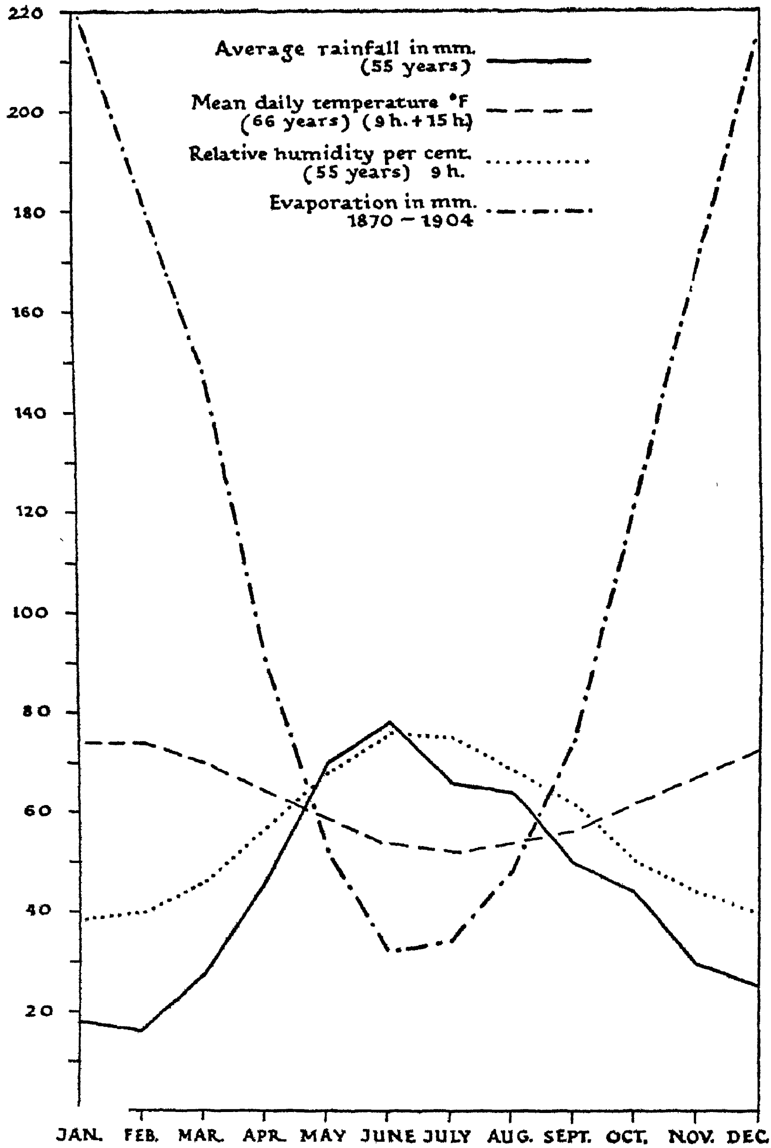

Fig. 138

Diagram to show the characteristics of Mediterranean climate. The data for this graph refer to the Southern Hemisphere, where midwinter comes in June

of the rain, and grows rapidly in the autumn and all through the winter. In spring, with rising temperature, falling water supply, and higher evaporation, it flowers quickly and seeds. The seeds are shed and lie dormant in the dry soil during the summer to repeat the cycle in the next twelve months. The plant evades the period of drought by forming seeds.

The Use of the Ephemeral Plant in Agriculture

Plants of this type can and do provide a mass of " feed " for a major portion of the year. Subterranean clover, so popular in many parts of Australia, is an outstanding example of an annual of the " drought evading class." An area of pasture land once sown with " sub " clover and provided with phosphate becomes " permanent." Each year the pasture regenerates from the seed left after grazing. This is the case of a permanent pasture based on an annual plant !

Adaptations seen in Ephemeral Plants

A number of secondary adaptations are seen in the ephemeral plants attuned to this periodic climate. The most important one is the appearance of a high transpiration coefficient. This is the weight of dry matter produced per unit weight of water transpired.

Others pertain to the seed. Hard seeds are profusely produced by many " Mediterranean " species. The advantage to the plant of hard seeds lies in this. In the event of a temporary breaking of the drought (" false rains ") all the seeds in the soil do not germinate promptly to produce seedlings which would die in the subsequent drought. Some remain dormant for the oncome of the true rains. The principle would seem to be that of not putting all the eggs in one basket !

Water-binding substance like mucilage (*e.g.* plantain seed) or epidermal hairs (*e.g.* cotton) may be produced on the external surface of the seed. These, once wetted, serve to maintain round the seed a body of bound water. In the event of premature rainfall these seed-coat modifications hold water from the drying soil, and though germination is retarded the seed does not dry out.

A system of agriculture has grown up to exploit areas under this periodic climate. Many square miles of territory in Australia are being rendered increasingly productive by pastures based on drought-evading species.

There are other responses to the Mediterranean climate, such as the bulb and corm, but these are not significant in agriculture. The olive tree, with a quite different response mechanism, is also a member of this plant community.

The Drought Exploiter

A response to another type of difficult water conditions is seen clearly developed in lucerne. The natural habitat of this type of plant is where the air is dry, the top layers of the soil dry, but down in the subsoil sufficient water reserves exist.

The plant has a very deep tap-root, which in nature branches but slightly until it reaches the low water-table. The shoot of the plant, like that of the drought evader type already described, is not morphologically adapted, but has the general appearance of an unmodified mesophyte.

How the Drought Exploiter Functions

Such a plant, once established in its natural home, has something of the following daily history. With the first light of morning the stomata open and food synthesis commences. Transpiration is rapid as a result of a highly efficient gas-exchange mechanism. In order to get carbon dioxide in, water vapour must be allowed to go out to the dry air. The plant has a high photosynthetic efficiency ; much dry matter is formed for the amount of water exhaled. With the advance of the day a water deficit arises in the tissues as a result of the inability of the water gradient in the soil to supply the demands at the root. Slight wilting supervenes, and the stomata close. Gas-exchange at once is considerably reduced, so that both transpiration and food synthesis cease. After nightfall the temperature drops and the water strain in the plant relaxes. The various diffusional water gradients concerned in supply, particularly the one in the soil, then overtake the demand. Conduction to the shoot is rapid, and the plant becomes turgid again, ready to repeat the daily cycle. Under these circumstances the total yield of the plant in terms of dry matter per day is not high. The restrictive effect of water supply, by enforcing a lowered gas-exchange for a part of each day, reduces the time during which synthesis is active. The high efficiency of the plant is not sufficient to compensate for this loss.

The Drought Exploiter under "Easy Conditions"

When this type of plant is grown in an area of easy water conditions (mesophytic conditions) the whole day is available for food synthesis. In such an area the stoma pores are not compelled to close for part of the day. The result is that the high efficiency of the plant is employed during the whole period of illumination, and enormous yields of dry matter per acre are produced.

Like the drought evader type, lucerne and other plants of similar character have developed secondary adjustments. The production of hard seeds is one.

At one part of its life lucerne cannot compete with any mesophyte, but in the remainder of its history it can smother almost any competitor. The reason for this is that in the seedling stage lucerne expends its food stores in developing root before producing shoot. After the two cotyledons arrive above the surface of the soil very little shoot is developed for a comparatively long time. All the reserves from the seed are expended in sending the tap-root down towards the deep-lying soil-water. The plant above ground remains quite tiny for a long time. Even under easy water conditions the lucerne still "remembers" the habits of its ancestors and continues to behave in the same way. During this period while the root is elongating and the shoot remains short the plant is easily smothered by mesophytic weeds, which develop their roots and shoots together. Once past this seedling stage, owing to its high efficiency, the growth of the lucerne is very fast, and it now competes with success against the most aggressive mesophyte.

This is the reason why lucerne must have a very clean seed-bed if it is sown broadcast. When the crop is sown in drills any weeds which appear can be kept down by inter-row cultivation until the lucerne plants have developed their roots and take care of themselves. Plants similar in nature to lucerne may yet await discovery in the arid regions in which it was evolved, and will prove valuable additions to the crop plants of the world.

The other kinds of modification to drought conditions may be briefly mentioned. The plants showing them are not particularly useful in agriculture.

The Succulent Plant

There are the succulent plants exemplified by many cacti, some of the *Senecios*, and members of other genera. These plants are found in areas of "fickle" rainfall where there is no marked periodicity, and no rain may fall over long periods of time. In these plants the trend of evolution is towards a reduction of surface to mass ratio. The leaves are few and small, or in extreme examples absent altogether. The stem shortens and increases in girth so as to approach to the spherical in shape. The cuticle is considerably thickened. The root system is confined to the surface layers of the soil. In the cells of the plant the sap has quite a low osmotic value, but the plant is full of a highly hydrophilic mucilage. The internal tissues show a diurnal variation in acidity, being more acid at night and less so by day. Gas-exchange is limited by the fewness of the stomata and the thick cuticle. Transpiration is low, and growth of the plant in its natural habitat is slow.

How the Succulent Plant Functions

The hydrophilic mucilage binds water strongly, and water once inside the plant is strongly held. Carbon dioxide intake is low, but the supply is conserved because by night the products of repiration are not breathed out but saved for re-use in food-making the following day. It is the accumulation of these products of respiration which causes the acidity of the tissues to rise during the night. The shallow root system allows the plant to absorb quickly any small amount of rain that may fall on to the dry soil. The succulent plant has difficulty in obtaining the materials for food-making. What it does get it holds on to, but dry matter accumulation and growth are slow.

The Drought Tolerant Plant

One plant of the desert which attracts considerable attention from the academic botanist is the creosote bush. In the intense drought of the south-western desert of the United States of America this plant simply dries out and tolerates advanced wilting. The leaves lose the greater part of their water content, but remain on the plant dry and leathery. When the rain comes the tissues re-hydrate and again become functional. Drought resistance in this case derives from the ability of the tissues to

remain alive but quiescent though dried out. A point of interest is that anatomically these leaves do not suggest drought resistance, rather the reverse.

Minor Adaptations

The whole field of adaptation to difficult water conditions is one of great interest, and a number of the less spectacular responses may be noted.

In some plants the leaf blades normally drop off and the petioles have become modified to form flat, leaf-like structures (phyllodes). In others the leaves have become reduced to small scales, but the stems flatten out to resemble leaves (cladodes). Both these adaptations are successful because in effect they shorten the path between the main vessels and the transpiring tissues.

Many plants (including many grasses) growing under dry conditions have bristle leaves. Many of these bristles are due to a normal flat blade becoming rolled to form a tube-like structure. The upper surface of such a leaf has many ridges, and in the epidermis of the furrows there is a line of very thin-walled giant cells.

In a moist atmosphere these "hinge-cells" or motor tissue are fully turgescent, and the blade is flat. When exposed to dry air the uncuticularized hinge-cells lose water and decrease in volume due to partial wilting. This has the effect of rolling the leaf into a long tube with the stomata (all on the upper epidermis) inside. The stomata are now enclosed in an isolated little atmosphere from which there is little or no diffusion, and transpiration is cut down. In certain plants the rolling has become permanent, and the leaf cannot now unroll.

Other bristles-like leaves or needles such as are found in many pines are formed by a considerable reduction in the transverse dimension of the upper surface. These are solid, not tube-like, so that all the mesophyll is concentrated round the main vein.

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CHAPTER XIII

THE INTAKE OF MANURIAL SALTS

The Region of the Plant Involved

THE intake of manurial or nutrient salts is carried out in the plant in the same region of the root as water intake, namely, the region bearing root-hairs.

Before intake is possible the salts must be in solution, and therefore free to diffuse. If the molecules of any one solute are to diffuse into the plant there must be more of that kind free outside the cell than there are inside. A concentration of any particular kind of molecule greater outside the cell than inside does not invalidate what has been said in regard to water intake. Just as the water molecule concentration in a solution is lowered by all the solute molecules present, so is the concentration of any one solute reduced by all the other solutes *and* the water. The key to the problem lies in the statement that each kind of particle diffuses on its own gradient. The direction in which water molecules are diffusing does not affect the direction in which a solute molecule is diffusing, except in so far as either affects relative dilution.

Intake of Solutes

The protoplasmic lining of the cell is an imperfect semi-permeable membrane and is permeable to many solutes. Hence, if the protoplast is permeable to a given salt molecule (or ion), and there is a gradient of concentration inwards of that salt, entry is effected. These two factors—degree of permeability and the presence of a gradient—are of fundamental importance.

A simplification may be pictured as in Fig. 139. The percentage concentrations shown refer to numbers of individual molecules. The arrows indicate the direction of diffusion in each case.

At one time or another nearly all of the known elements have been found during the analysis of plant material. This does not mean that all these are used by the plant, but simply that they have been in the soil solution and that the plant's protoplasm has been permeable to them. The plant is not selective. Selective absorption by the root is not possible, for if a diffusion gradient

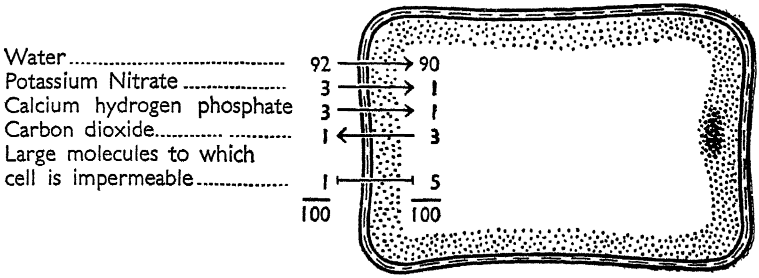


FIG. 139—Dialysis (simplified)

The figures for the various components of the system represent molecular concentration. The arrows show the direction of diffusion

of a substance exists and the proloplast is permeable to it it will enter. Certainly, if a salt molecule once inside the cells of the plant is taken out of the diffusional system, as by being " built into " another more complex molecule or is adsorbed, then the inward end of the gradient remains low. This will delay or postpone indefinitely the attainment of equilibrium between the plant's sap and the soil solution, and the gradient will not flatten out. In these cases when the molecule is immobilized by adsorption, or taken out of the diffusional system by chemical action, more of the substances will appear in the plant, and an appearance of preferential or selective absorption is suggested. The point here is that as regards entry the living cells cannot pick and choose from amongst a mixture of molecules in solution to all of which it is permeable.

The term osmosis should be used only to describe the diffusion of the solvent of a system across a semi-permeable membrane. The term *dialysis* should be preferred in describing the passage of a solute.

Once a solute molecule or ion, diffusing in the soil-water, has approached the root hair, it may proceed into the tissues by the same routes as a water molecule, and diffuse through the water of the colloidal cell walls or dialyse from cell to cell. The path for such a diffusing unit is along the water continuum. Eventually it will reach the water in the xylem. There it will be carried up in solution by mass flow. Thus, water and dissolved salts are conducted to the shoot tissues for distribution amongst the mesophyll cells by diffusion. Transpiration takes off the water, and the salts are left for purposes of synthesis. The final result is very similar to concentration of a solution by evaporation.

Selective Accumulation in the Wider Sense

Two main amendments to the simple mechanism outlined above must be mentioned. The first of these is what has been referred to as selective accumulation, and sometimes as " heaping up." In general, either of these two terms applies to all cases where the plant on analysis is found to contain more of a given ion or molecule than seems justified by the very weak concentration available to it in the culture medium. Analysis of a nutrient solution after a plant capable of selective accumulation has been growing in it for some time suggests that selective absorption has been going on. Fig. 140 shows the alteration in the composition of a water culture medium in which barley plants had been grown for twenty-four hours.

The simplest case, and one to which the terms can only just be applied, occurs when an ion is used in building up a more complex molecule, which is part of the fabric of the plant. For example, when nitrate is used to make protein.

A rather more special case is when the element, once inside the cell, is precipitated by chemical action and becomes " matter

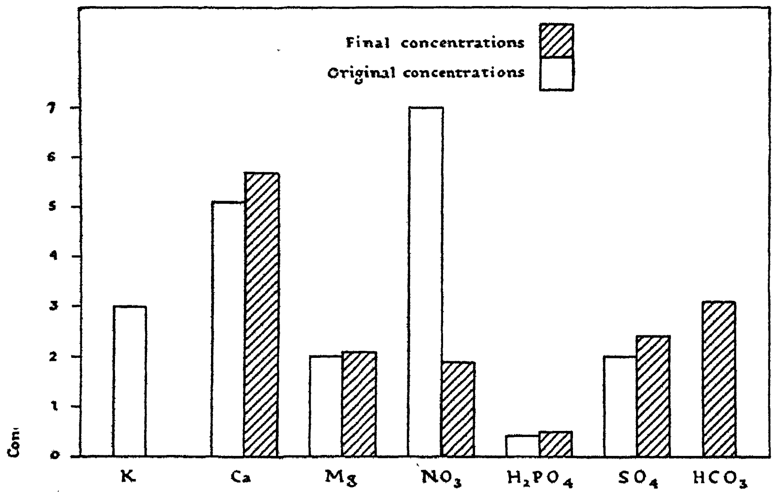


FIG. 140

(*From D. R. Hoagland, Inorganic Nutrition of Plants*)

Changes of concentrations in a nutrient solution as barley plants absorb water and ions. Relatively, a greater quantity of the ions than of water is absorbed in some cases, so that the solution is diluted. This is notably true of potassium ions in the above experiment of 24 hours' duration. The concentration of potassium sank almost to zero. Some ions increase in concentration, because water is absorbed in relatively greater amount than ions.

in the mass." The units of the precipitate are too large to be mobile. The actual gradient is in fact kept low at the inward end, and diffusion continues as long as precipitation within the cell is possible and there is a supply of the particle in solution outside.

Another case arises where the substance taken in is adsorbed on a surface inside the plant. Here, too, the particle is immobilized and taken out of the diffusional system. Again the net result is that diffusional equilibrium cannot be attained or is delayed.

Selective Accumulation in the Narrow Sense

The case where the term selective accumulation applies in the strict sense occurs when the concentration of any particular ion *in solution* inside the cell sap is higher than the concentration outside. That this is possible is well seen in Fig. 141, which re-

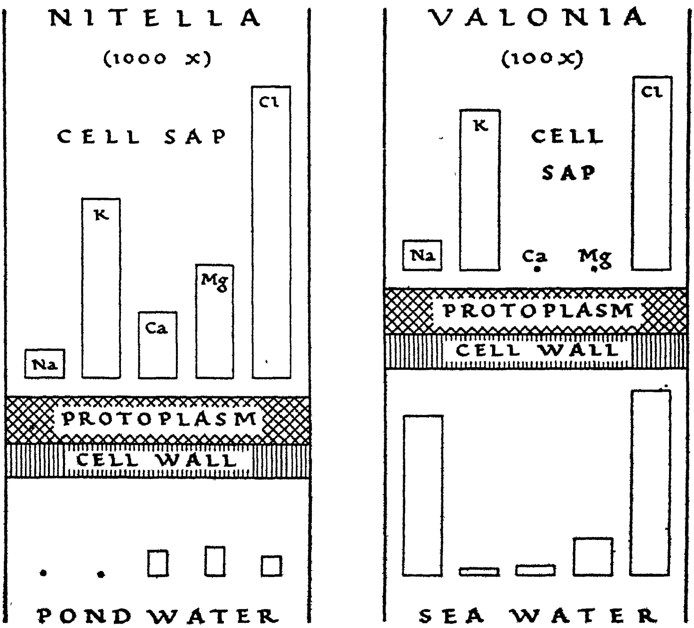


FIG. 141

Selective Accumulation

Diagrammatic representation of relative concentrations of several ions in the culture medium and in the vacuolar sap of *Nitella* (a fresh-water plant) and *Valonia* (a sea-water plant)

(*From D. R. Hoagland, "Inorganic Nutrition of Plants"*)

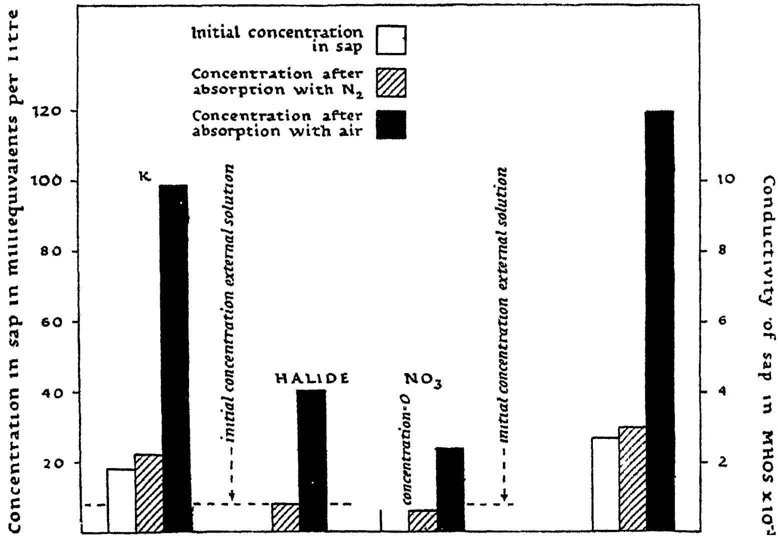


FIG. 142

Selective Accumulation

Showing necessity for oxygen. Compare the amounts accumulated when oxygen is present with those when oxygen is replaced by nitrogen

(Material is excised roots of barley)

(*From D. R. Hoagland, "Inorganic Nutrition of Plants"*)

presents results obtained from two algæ, one fresh-water and the other marine. The semi-permeable membrane is represented as separating the two solutions ; the value of the ions are shown graphically. The substance continues to enter against the gradient. The explanation of this phenomenon is not simple and not yet complete, but it is clear that in achieving this condition the plant expends energy.

Accumulation against the gradient can only take place where energy release or respiration is active. That means there must be a supply of material which is usable as a " fuel " in respiration, and there must be oxygen present. Fig. 142 shows the effect of aeration on accumulation of potassium by roots of barley plants, while Fig. 143 shows both aeration and fuel (sugar) consumpt. When these conditions suitable for release of energy are satisfied certain ions are accumulated, and the cell sap contains *in solution* a higher concentration of these particles than does the external medium. Physically this is equivalent to making a body travel uphill.

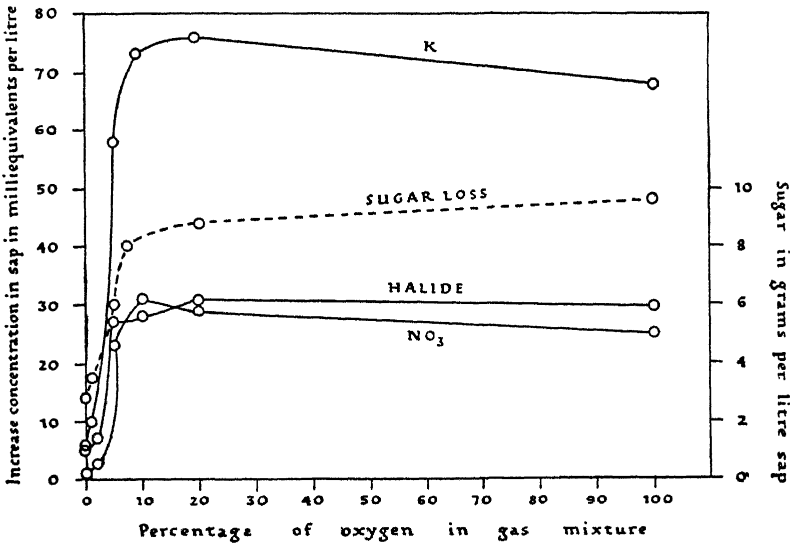


FIG. 143
Selective Accumulation
Showing the necessity for food and oxygen
(Material—excised roots of barley)
(From D. R. Hoagland, " Inorganic Nutrition of Plants ")

A number of factors in addition to food and oxygen supply affect the amount of solute forced in. Examples of these are temperature, transpiration rate, hydrogen ion concentration of the medium and the stage of growth of the plant.

Fig. 144 presents evidence which shows that the requirements of the plant for individual ions varies considerably during its life cycle.

From the point of view of the grower of food this aspect of intake is important. Plants capable of selective accumulation will have in their tissues a reserve of solute if at any time the supplying power of the soil or the intake capacity of the root should temporarily fall below requirements.

Another facet of this question of selective accumulation is recognized when it is remembered that the soil often has a considerable power of holding many ions out of solution, either by adsorption or included in a but slightly soluble compound. Potassium and phosphate are common examples. There may be abundant supplies of such substances in the soil, but only a very small proportion of them in solution and available to the

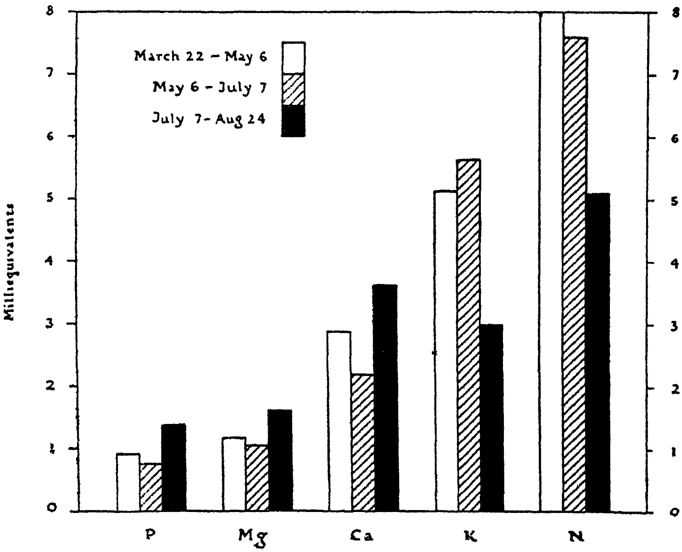


FIG. 144

Selective Accumulation

To show the average daily absorption of nutrient elements by a tomato plant at various stages of growth from an aerated solution

(*From D. R. Hoagland, " Inorganic Nutrition of Plants "*)

plant. Movement into the plant of the few ions actually in solution will cause others to be released from the reserves locked up in the soil. Selective accumulation in the plant, by maintaining the concentration of such an ion in the soil solution always at a minimum, causes a smoother release from the soil complex and builds up a reserve in the tissues readily available to meet any demand. In general, selective accumulation is to the plant what a cistern of water in the loft is to a house with a poor supply from the main pipes.

Interference between Particles at a Membrane: Antagonism

The second amendment to the simple diffusion theory of salt intake lies in the fact that certain pairs of ions affect each other in their entry into, or passage across, a membrane. For example, if a high proportion of magnesium be present in the culture medium offered to a plant, injury is caused to the living cells of the root. This is due to a poisoning effect of magnesium. The

locus of the poisoning is in the cell protoplast, probably at its surface, and acts possibly by altering the balance between the solid and liquid phases. When, however, sufficient calcium is added to the medium the poisoning effect does not appear. Calcium is here said to act as a *depoisoner*, and the two elements are said to be antagonistic. The calcium does not reduce the amount of magnesium ; it merely prevents its effect. The calcium probably acts by effecting repair of the protoplast or preventing the initial damage.

Elements which show Antagonism

A number of antagonistic pairs are known ; for example Mg/Ca, S/Se, and Na/Ca.

It is to be made clear that it is not the absolute amounts of the poisoner and its depoisoner which may be present that are important ; it is the ratio between the two. For example, in the reduction of the severe ill-effects caused by magnesium it has been shown that the percentage of injured leaves on a plant decreased as the Mg/Ca ratio increased from 1 to 50. Experiments with a number of crop plants yielded data of the same type. It has been shown that the dry weight of tops of wheat plants were inversely proportional to the logarithm of the Mg/Ca ratio between the limits 1 and 50 of the ratio.

BOOKS FOR FURTHER READING

HOAGLAND, D. R. *Inorganic Nutrition of Plants* (Chronica Botanica Publishing Co., Waltham, Mass., U.S.A., 1944)

UBER, F. M. " Microincineration and Ash Analysis " (*The Botanical Review*, 6 (5), 1940)

STILES, W. *Trace Elements in Plants and Animals* (Cambridge University Press, 1946)

Chapter XIV

THE ELEMENTS WHICH PLANTS USE

The fundamental mechanism of salt intake outlined in the previous chapter must now be related to practice. The matter is important, for it is now recognized that estimation of the carbohydrates, fats, and proteins in a food is not a complete index of its value. The total ash (mineral) content and the proportion in which each component of it occurs is also very significant.

Estimation of Mineral Intake

Consider first the methods by which the rate of entry and amount entering the plant of the various components may be followed.

Two main lines of investigation may be recognized. On the one hand there are methods of chemical analysis, and on the other methods in which the reaction of a plant indicates the state of affairs.

Chemical Methods

Description of the detailed methods of the chemist are not within the province of this text. Briefly, the material of the plant body is first sampled, and a quantity dried in an oven to constant weight. The loss in weight indicates the water content. A more positive result may be obtained by distilling off the water with such a solvent as naphtha.

The dry matter remaining from the oven test may be used for the estimation of the major food classes, but a weighed portion should be incinerated to provide the ash. The ash is analyzed by suitable methods to reveal the proportions of each component present.

There are available in the literature many examples of data obtained from this kind of work. Some of these carry the investigation to very fine limits.

Water Culture : Hydroponics

Another way in which purely chemical procedure may be employed lies in growing a plant in a medium of known composition, and after a period analysing the medium. This shows

A Typical Succulent Xeromorph

Phyllodes

The petiole of each leaf has flattened out; the much-divided blades will soon fall off

Simple Apparatus for Continuous Flow Culture

The fresh solution siphons from the reservoir on right to the culture jar. The overflow passes by siphon to waste on left

(*From Shive & Robbins. Bull. 636, New Jersey Ag. Expt. Station*)

which components have been taken by the plant and what quantity of each.

Plants live and do well when their roots are immersed in a solution of mixed chemicals of appropriate strength and composition and so a technique of "water-culture" or "solution culture" is commonly employed. So successful is the method that it has been adapted to commercial crop production, and is now called the science of hydroponics. One disability of water-culture in experimental work is that the solutions are necessarily weak, and a component in demand by the plant is soon in deficient supply, thus upsetting the mineral balance of the solution. To obviate this the liquid in the culture jars should be changed often, or better still, the plant grown in a stream of fresh culture solution flowing steadily round the roots from a reservoir. Sometimes the plants are grown in clean, well-washed sand, moistened with the known solution.

In many investigations both the plants and the culture solution in which they grow are analysed. Plants grown in a solution of known composition (the changes in which are followed) are at the end of a period themselves analysed.

A further refinement has been introduced. Radio-active isotopes of certain elements are used in the formation of the mineral compounds to be offered to the plants. The presence of such isotopes may be readily detected at any time. Hence a radicle or ion with such an isotope is " tagged " or " labelled," and its path into and through the plant may be followed.

Biological Methods

Turning now to the methods by which the reaction of the plant is used to reveal the state of affairs. The first of these is to use some special plant as a " living reagent." For example, certain strains of the common mould fungus *Aspergillus niger* can be used to estimate the copper content of a soil. The colour of the spores of this plant are white when no copper is present. In the presence of 1 part of copper to 200 million parts of soil the spores are orange-yellow. The spores become light brown with 2 parts per 200 million, while, in concentrations up to 1 part in 16 millions, the spores produced are dark brown or black (Colour Plate XVII). The results are obtained in five days. The same species of mould may also be used to test for magnesium deficiency. After five days

in a nutrient medium complete except for magnesium this fungus made no growth. In exactly the same medium, but with 25γ magnesium added (as $MgSO_4 7H_2O$) slight sterile growth appeared. In similar media, but with increasing amounts of magnesium added, the growth of the fungus improved and the number of spores increased. This is clearly seen in Plate 94.

Injection Methods

More usually it is one of the higher plants that is used in this type of test. When a crop appears "off colour" or shows some pathological condition, and some maladjustment of the mineral supply is suspected as the cause, a series of pure chemicals, each in separate solution, may be injected into it.

Injection may be carried out in a number of ways. Merely painting a leaf or fruit with an appropriate solution of a salt will cause a local response. The molecule in deficient supply diffuses from solution through the cuticle. In other cases the tip of a leaf is cut off under a test solution as in Fig. 145. The solution "runs back," and that solution which remedies the defect in the leaf is soon identified. The fluid may feed in through the stump of a cut leaf stalk (Fig. 146).

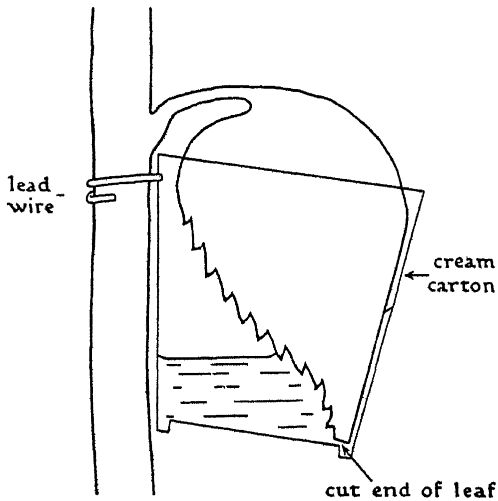


FIG. 145

Plant Injection through cut leaf-tip

(From W. A. Roach, 1938)

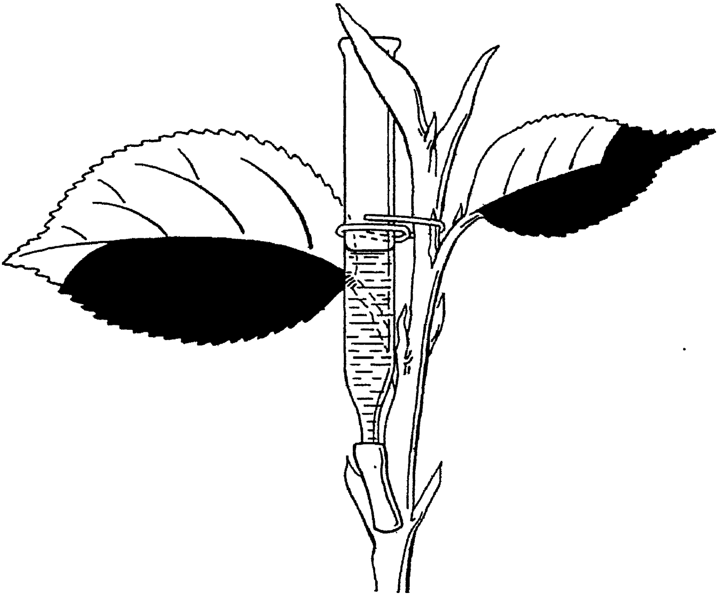


FIG. 146

Plant Injection

A glass tube containing solution is connected by a rubber tube to the cut end of a leaf-stalk

(*From W. A. Roach, 1938*)

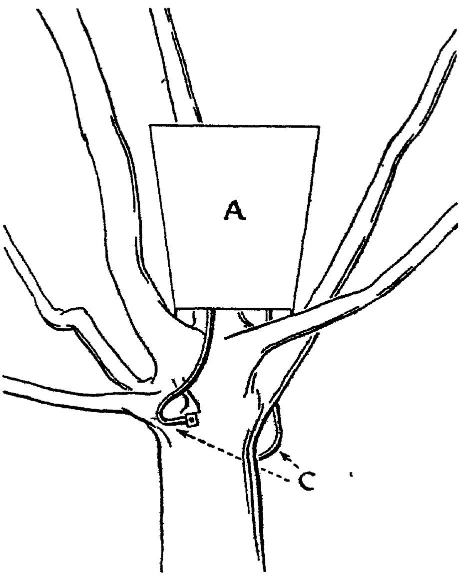


FIG. 147

Plant Injection

A whole tree is supplied from the reservoir through an auger hole in the trunk

(*From W. A. Roach, 1938*)

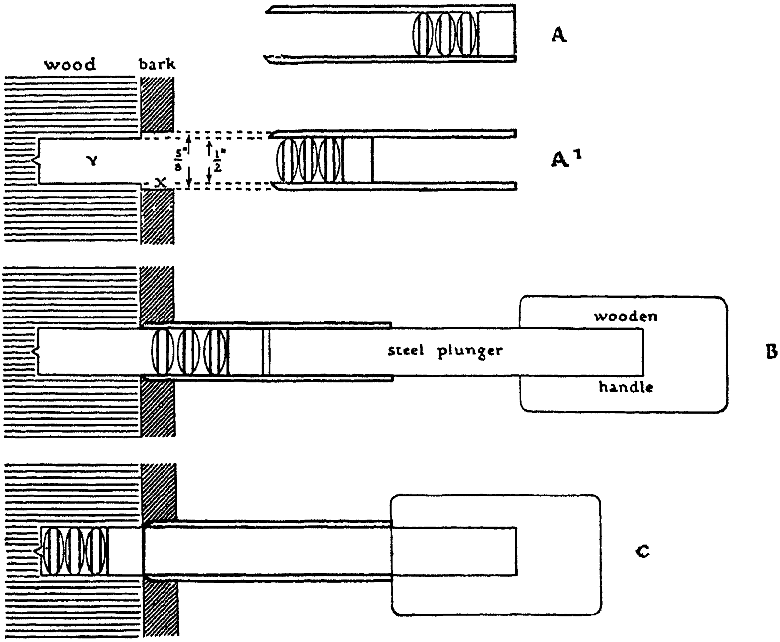


Fig. 148

Plant Injection

A tree may be injected (for diagnostic or curative purposes) with pellets of appropriate chemicals forced by a " gun " into an auger hole

(*From W. A. Roach, 1944*)

In the case of a woody tree an auger hole is bored in the trunk. Into this is led a supply pipe from a reservoir of appropriate solution (Fig. 147). After some time the transpiration pull draws the solution into the xylem, and so up into the leaves. In other cases pellets of appropriate chemicals may be forced into the wood of the tree trunk. There they dissolve in the sap and are carried to all parts of the plant. This is shown in Fig. 148. When appropriate chemicals are used a response is seen in the tree.

The Elements used by the Plant

By employing one or other of these various methods it has been established that plants must get from their environment, in quantity, carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, calcium, magnesium, along with a smaller quantity of iron. The source of hydrogen and oxygen is the

water supplied from the soil. Oxygen is also supplied from the air. The green plant uses only carbon dioxide gas from the air as a source of carbon. The carbon of the organic matter in the soil is not used. It seems strange that an organism built entirely of carbon compounds should be limited to such a meagre source of the element, for the gas occurs in the atmosphere to the amount of only three hundredths of one per cent. There is little doubt that green plants could use more carbon dioxide than occurs naturally in the air. Nitrogen, on the other hand, is abundant in the air, but this is not used as a source of supply by the green plant. Certainly, some of the lower plants such as bacteria and fungi do use gaseous nitrogen, but all of these have a source of energy other than light. Nitrogen for the normal green plant comes only from the inorganic nitrogen in the soil. Seeming exceptions to this are those green plants which live in association with bacteria or other lowly types. All the other elements listed above, *e.g.* sulphur, phosphorus, potassium, calcium, magnesium, and iron, under normal conditions are derived wholly from the soil. There is evidence from spraying and painting experiments that the shoot can absorb inorganic salts. As there is rarely any natural source of supply of these to the shoot, this may be ignored.

Elements are never absorbed as such, they must always be offered to the plant in combination. They enter in either molecular or ionic form. They must be in the dissolved state, and therefore free to diffuse. In the case of most elements all inorganic combinations are not equally suitable, and the plant appears to be strict in its requirements. For example, all the evidence points to phosphorus being taken only as a phosphate radicle or ion, sulphur probably only as the sulphate, and so on.

Elements which are required in quantity, so that a poor crop results if they are not present in substantial amounts, are called *essential elements* in the nutrition of plants. When one crop seems to demand a relatively larger amount of a particular element than other crops do, that element is called the *dominant* ingredient for that crop. Thus in crops grown for leaf (cabbages, kale, etc.) nitrogen is required in more quantity than is necessary for, say, mangolds, which seem rather to require a higher proportion of potassium. Nitrogen is regarded as the dominant ingredient for kale, while potassium is the dominant for mangolds.

Interest next focuses on certain elements such as arsenic and

copper, which at one time were regarded as entirely deleterious to the plant's health, and indeed could cause death. These substances were classified as *toxic elements.* Many of our weed-killers or herbicides have developed from studies on these plant poisons.

Other elements which appeared to have no effect when present were referred to as *passive* or *inert.* For a time the elements available to the plant were classified into essential, toxic, and passive.

Elements required in Small Amounts

Early in the 'twenties of this century (about 1922) evidence came forward that this classification was invalid. Largely through refinements in methods of water culture and improvements in the purification of salts, it was discovered that very small quantities of some elements, previously classified as poisonous or passive, are absolutely necessary for the growth and development of plants. The difference between these elements and the essential elements, so far as this discussion has gone, lies only in the amounts required of each.

Minor or Trace Elements

The name to be used for this class of elements essential for the health of the plant, but required only in very minute quantities, has not yet been established. Minor, micro- or trace elements have been proposed. A further term, micronutrient element, has been suggested, but has not been widely adopted, for there is no proof that they all enter into nutrition in the strict sense. There is something to be said for and against the use of each of the four terms, and here " minor " will be adopted. The use of the term " rare " element in this connection is definitely to be deprecated.

Many of the elements previously classified as poisonous or toxic, when supplied in sufficiently high dilution, are now found to be essential. These are the minor elements. By small quantity or high dilution is meant from about 0·01 milligrams up to a few tenths of a milligram per litre of nutrient solution, or round about one part per million.

Deficiency of supply of such minor elements as boron, manganese, and copper cause pathological symptoms in the plant, and " disease " associated with over- or under-supply of nutrients will be considered later under pathology. Only the functional rôle of the various elements will be discussed now.

Quantity or Balance in Nutrient Supply

The elements absorbed through the roots and required for the complete nutrition of the plant (and eventually for the animal) form a series, graduated on the basis of the quantity required. Quantity in this regard should not be used in an absolute sense but rather in the sense of ratio. Too much of one may impose deficiency of another. Imbalance of the components of the nutrient solution presented to the plant is rather the better view. This concept of imbalance applies to all the elements required by the plant for full health, and not to minor elements only.

It must be stressed that a statement about deficiency of this or that element in the soil often does not necessarily imply complete absence of the substance. Rather it implies an insufficient proportion of available soluble compounds of the particular substance in question. Any compound which is insoluble or otherwise prevented from diffusing is not available. For example, soil colloids adsorb or bind potassium, and the amount of this bound material available to the plant depends, not on the total amount present in the soil, but on how far the colloidal material is saturated with it.

Factors affecting Ash Content

The total ash content and the relative proportion of each element found in the plant is conditioned by a number of circumstances. The first of these is the nature of the plant concerned. Two plants of the same kind growing in the same soil may be indistinguishable in appearance, yet differ in ash content. These two belong to different physiological strains or varieties of the plant. Secondly, one and the same plant growing continuously under non-varying conditions may differ in ash content and composition at different stages of growth and in different organs. Again, the nature of the supply to the plant from the soil or culture medium affects the nature of the ash. It is of interest that different plants offered either soluble or insoluble supplies of the same element show differences in ability to use them. Furthermore, addition of supplementary manures may not increase the ash in the plant. For example, if a fully fertile soil is used as a culture medium, the addition to it of soluble phosphate will not increase the amount of phosphorus in the tissues of the plant growing thereon.

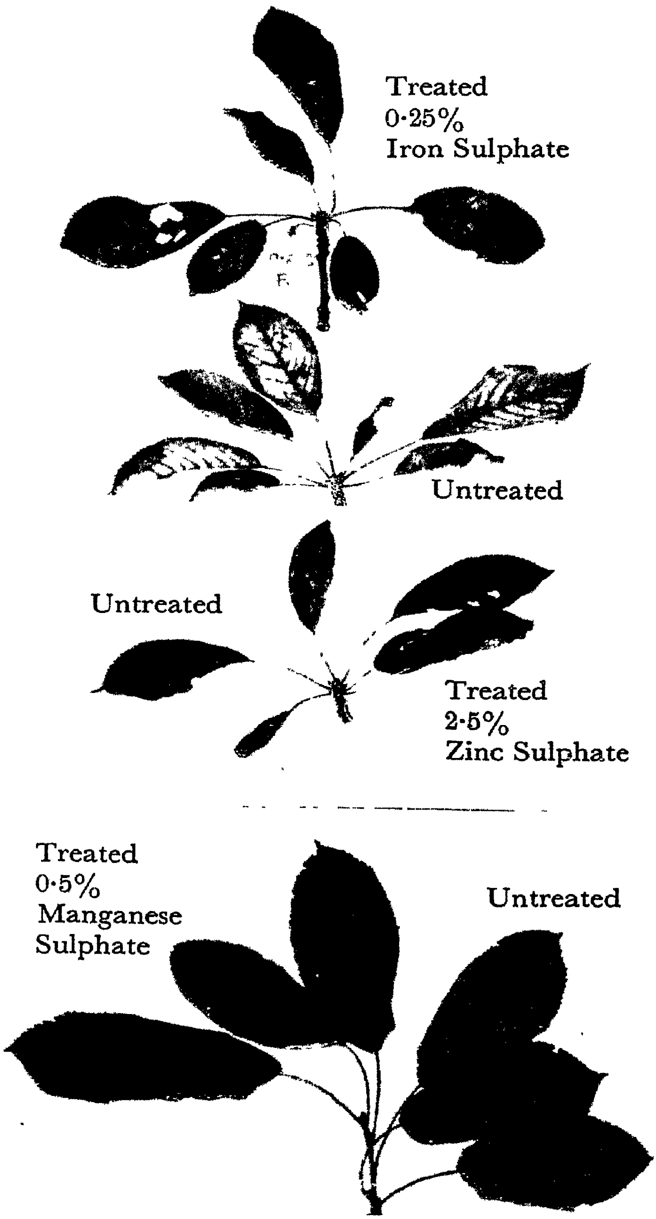
The water content of the soil, too, or the molecular concentration of salts in a liquid medium affects the total ash percentage and the proportions of each component in the tissues.

The effect of species must be interpreted always with regard to the fact that there may be genetical strains within the species. When this is so, the plant selector or breeder can intervene and develop specialized races. At the moment the more gross plant unit, the species, will suffice for consideration. An even larger unit may suffice for more extreme differences. For example, clovers and their allies (legumes in general) have a higher total ash content than the grasses growing alongside them. So, too, the clovers tend to have a higher proportion of lime to phosphorus, while the grasses have a higher phosphorus to lime content. The Ca/P_2O_5 ratio therefore tends to move towards calcium in the legume and towards phosphorus in the grasses. Within the grasses the kinds which normally constitute bog hay (a mixture of natural grasses found on poor, rather acid soils) have a lower total ash content than the better grasses found in the sown fields.

A complete study of this subject is due to workers at the Waite Research Institute in South Australia, and the data discussed here will be taken from their work. Experimental plants were grown in large, glazed earthenware pots. The soil used was a well-known type whose behaviour is understood. A gravel mulch some quarter of an inch on the surface of the soil reduced evaporational losses of water to the minimum. By adding weighed quantities of water the soil was maintained through the period of the experiment at 60 per cent. of its total water-holding capacity. The course of transpiration was therefore easily followed from the results of periodical weighings of the pots. The plants were kept under experiment right through their life cycle up to the commencement of flowering, and hence loss of nutrients, ash, etc., from pollen-shedding, withering, and severance of leaves and flowers was obviated.

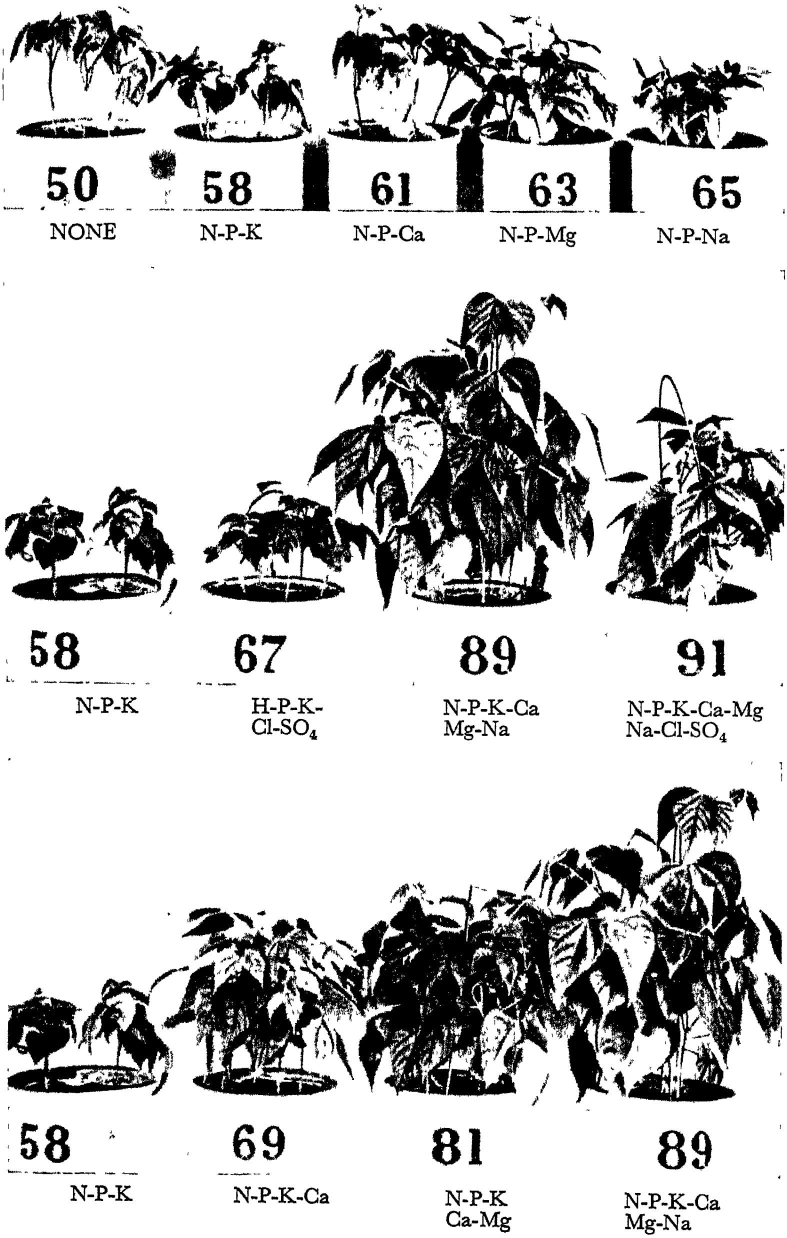
The behaviour of the plant as a whole is given in summary form in the table on page 315. Total yields are given in column 1. It is seen that in this respect species differ very considerably. These figures are in conformity with general observations made in the field. The three cultigens, *Lolium subulatum* (a ryegrass), *Trifolium subterraneum* (a clover), and barley (a cereal) easily outyield the "natural" plants included in the experiment.

PLATE 59 DIAGNOSIS OF MINERAL DEFICIENCY



Leaves of Cherry Trees growing on deficient soil respond when painted with appropriate solutions
(*Copyright, East Malling Research Station*)

PLATE 60 IMBALANCE OF MANURIAL SALTS



Addition of manurial salts by accentuating deficiency of others may depress crop yield (*From R. L. Carolus, "Plant Physiology," 13, 1930*)

Species	Dry matter produced (grams)	Amount of water transpired (litres)	Transpiration ratio	Percentage of nutrients in dry matter								Grams assimilated per litre of water transpired	
				N	P_2O_5	CaO	K_2O	Na_2O	MgO	Cl	Soluble ash	N	P_2O_5
Danthonia penicillata	28·51	10·17	355	2 28	0·41	0·45	2 86	0·24	0 20	1 07	5·29	·064	011
Barley	106·25	27 28	257	1·69	0·34	0·57	4·32	—	—	—	10·19	·066	·013
Erodium botrys	11·78	3·00	256	4·08	1·07	4·18	4·48	1 66	0·93	1 87	13·77	160	042
Lolium subulatum	122·17	40 29	330	1 72	0·58	0·71	4·53	0·98	0 39	3·35	9·77	·052	·018
Trifolium subterraneum	74·40	32·35	435	3·45	0·61	2·35	4 01	1·54	0·57	1·86	11·83	·079	·014
Atriplex vesicarium	26·63	9·59	360	2·43	0·93	1·87	6·67	5·76	1·03	5·23	22 87	·067	·026
Atriplex semibaccatum	35·19	7·36	209	2·58	0·68	1·31	4·75	3·55	1·27	3·37	15·47	1·23	·032

(*From Richardson and Co-workers, 1931*)

The position of the *Atriplexes* at the other end of the scale is worthy of comment. They appear to yield very poorly, but in their native habitat they have a value because they produce what they do when little feed is available from other sources. The high " soluble ash " content of these species further enhances their value. Only difficulties in the establishment of these plants would seem to prevent their cultivation in suitable areas. The position of *Erodium* in the table is of interest. The difference in ash content between the clover and the three members of the grass family (*Danthonia*, barley, and *Lolium subulatum*) follow very much the general position already stated.

While remembering that these figures relate to plants as a whole at the flowering stage, it seems that the low yield of dry matter given by *Erodium* is important because it has a high content of each of nitrogen, phosphate, lime, and magnesia. The clover is runner-up in lime content, and takes a high place in regard to the other substances. The high phosphate content of *Erodium* and *Atriplex vesicarium* is interesting, and the value of these plants on this account is recognized by Australian stock-masters, who favour the plants for the beneficial effect they exert when eaten by stock.

As regards the calcium/phosphorus ratio the species reported on fall into three classes : one with a ratio about 1 : 0·25, another

with 1 : 0·5, and a third where the two are nearly equal. Such dissimilar ratios between different plants must be considered when pastures are being formed, as the proportion of these two elements present in the food of animals affects their health and development.

In the two columns to the extreme right of the table are seen some indication of the " efficiency " of the various plants as gatherers of mineral nutrients in proportion to the water transpired. This matter may not be of importance in areas well supplied with rain, but in drier climates it takes on a special importance.

The Use of Insoluble Compounds by Certain Plants

That the mineral content is not evenly distributed throughout the plant is shown by the table below. It is interesting to see here how phosphate and nitrogen migrate into the seed, while potash and lime remain more in the vegetative portion of the plant.

	Percentage D.M. on total dry weight	N	P_2O_5	K_2O	CaO
Erodium botrys :		%	%	%	%
Seeds	39·1	1·56	·93	—	—
Remainder of plant . .	60·9	·61	·17	—	—
Barley :					
Seeds	34·2	1·93	·61	·69	·05
Remainder of plant . .	65·8	·76	·09	4·00	·60

Proportion of grain at maturity, and contents of Nitrogen, P_2O_5, K_2O, and CaO present in the grain and in the remainder of the plant for (1) *Erodium botrys*, (2) barley (*From Richardson and Co-workers, 1931*)

It is essential that a substance be in solution before it can enter into an intact plant root. An element forming part of a compound which is insoluble in the soil water is not available to the plant so long as it remains unaltered chemically. Plant roots excrete certain ions which react with compounds in the soil, and so render available the components of these insoluble materials. For example, if a plant is grown in such a way that its roots come into actual contact with the polished surface of a slab of marble, it will be found after some time that the roots have dissolved away the calcium carbonate wherever contact has been made. The polished surface will show an etched tracery

of the root. The root, probably by excretion of carbon dioxide, dissolves the carbonate.

That compounds other than calcium carbonate can be affected is brought out by the following table. This gives the results obtained from growing three very different plant species in complete water culture. Two different sets of solution were used. In one the phosphate was supplied as tri-calcic-phosphate (insoluble), and the other as mono-calcic-phosphate (soluble).

	Dry Matter (grams)	Ratio Roots : Tops	% P_2O_5	Amount P_2O_5 (grams)
Lolium subulatum :				
Monocalcic series . .	34·57	1 : 3·3	·37	·128
Tricalcic series . .	28·29	1 : 4·3	·37	·051
Trifolium subterraneum :				
Monocalcic series . .	40 90	1 : 5·7	·35	·143
Tricalcic series . .	4·29	1 : 3·1	·35	·008
Erodium botrys (total) :				
Monocalcic series . .	31·13	1 : 17·4	·47	·145
Tricalcic series . .	24·74	1 : 15·8	·38	·094

Dry matter produced, percentage and amount of P_2O_5 assimilated by *Lolium subulatum*, *Trifolium subterraneum*, and *Erodium botrys*, under conditions of soluble and insoluble phosphate supply

(*From Richardson and Co-workers, 1931*)

Briefly, the figures show that neither the ryegrass nor the clover can make use of insoluble phosphate to any great extent while erodium can. In the case of clover, the yield of dry matter fell in response to the paucity of phosphate, but in such yield as there was the phosphate content was maintained. The ryegrass, when offered only insoluble phosphate, largely maintained its dry matter yield, but the percentage of phosphate dropped very considerably. The erodium largely maintained its yield and ash content in both the nutrient media. These three plants exemplify three general types.

A Plants which when offered only insoluble phosphate produce a reduced yield of normal herbage (*e.g.* clover).

B Plants which while not using insoluble phosphate keep up the yield of dry matter, and thus produce phosphate-deficient herbage (*e.g.* ryegrass).

C Plants which, presumably by their root action, can use insoluble phosphate, and so keep up yield of dry matter and mineral content (*e.g.* erodium)

Plants of the ryegrass type in a soil containing insoluble phosphate only, produce herbage which, while apparently feeding the stock well, is not supplying at least one essential element of the diet.

The erodium type of plant, if it were capable of producing a better total yield, would be of importance because it would provide a good crop of normal herbage on soil rich in insoluble phosphate but deficient in an available (soluble) form. Erodium is not the only kind of plant which falls into this class, and it would appear that these have a use on land deficient in available nutrients, but having a reasonable content of these in non-available forms.

Stage of Growth as Affecting Ash Content

The stage of growth of the plant is another factor affecting the percentage of mineral nutrients in the tissues. In experiments conducted at the Waite Institute "harvests" were made at six developmental stages, namely: (1) commencement of tillering; (2) active tillering; (3) advanced tillering; (4) plants in full flower; (5) plants with grain at "milk" stage; (6) plants fully mature.

The results are presented in the following table. These show that at each succeeding stage there is a progressive fall in the *percentage present* of all nutrients derived from the soil except silica.

Harvest	Date	No. of Pots	Water transpired	Dry Matter produced	Percentage composition of dry matter					
					Nitrogen	Total ash	Silica	Phos. acid (P_2O_5)	Potash (K_2O)	Lime (CaO)
			Litres	Grams						
1st	July 19	12	3·33	13·41	5·58	17·70	1·89	·904	7·35	1·07
2nd	Aug. 9	8	7·58	33·21	4·28	17·68	1·97	·639	7·25	·98
3rd	Aug. 30	7	15·11	65·78	2 57	15·00	2·02	·430	5·77	·73
4th	Sep. 20	5	27·28	106·25	1·69	12·17	1·98	·345	4·12	·57
5th	Oct. 11	6	38·98	148·70	1·23	9·23	2·05	·287	2·99	·42
6th	Nov. 9	6	44·68	165·53	1·18	8·89	1·83	·285	2·80	·40

Dry matter produced, percentage of nitrogen and ash constituents at various stages of growth of barley
(*From Richardson and Co-workers, 1931*)

Fig. 149 shows that for barley very little nitrogen and very little ash were absorbed into the plant after flowering; indeed, half the total nitrogen had been absorbed before tillering had become really active. As regards ash, half the total intake was accomplished before tillering had become advanced.

PLATE 61 SOLUTE INTAKE FROM INSOLUBLE COMPOUNDS

Tricalcic Phosphate Series	(D31	—Erodium Botrys—	D15)	Monocalcic Phosphate Series
	(D28	—Subterranean Clover—	D 8)	
	(D22	—Wimmera Ryegrass—	D 2)	

(From Richardson & Co-workers Bull 49, C S I R (Australia) 1931)

Apparatus for the measurement of carbon dioxide absorbed by a leaf in photosynthesis under natural conditions. Note cellophane bag chamber with thermometer at top right; cup chambers centre and bottom leaf

(*From Heinicke & Hoffman. Bull. 577, Cornell Ag. Expt. Station, 1933*)

With ryegrass and clover the curves are of slightly different shape, in that the major portion of intake comes rather later; this is shown in Figs. 150 and 151.

These differences between plants is summarized for the before-and-after flowering periods in Fig. 152.

The remainder of the data all go to show that the percentage of nitrogen and percentage of ash in the tissues fall progressively with age.

These changes in the chemical composition of the tissues are due to progressive changes in the proportions of the kinds of tissue elements present in the plant. With advancing age and development there is an increase in the amount of purely structural elements, such as sclerenchyma, xylem, and so on. These consist only of cell walls; they contain no living contents rich in nutrients. As the cells modify, the contents are broken down and translocated to younger areas.

It should be noted that these figures are *proportions*, and though the figures fall, the *total weight* of nutrients in the whole plant rises. This means that with advancing age of the plant the total amount of food increases, but that its "richness" decreases.

A second point brought out by these figures is that the amount of each mineral absorbed per unit of water transpired is highest in the early stages of growth, and falls off with ageing of the plant.

THE UTILIZATION OF DIFFERENT COMPOUNDS OF ELEMENTS

(1) *Nitrogen*

Let us now turn to the special characteristics of each element in connection with intake. It was believed at one time that the plant used nitrogen only as the nitrate ion NO_3, and that ammonia and other forms had to be converted to this radicle in the soil before entry or utilization was possible.

It is now known that in the field ammonia is used satisfactorily by some plants. Whether any particular kind of plant can make use of ammonia or not would seem to depend on whether it can "step up" this form of nitrogen quickly to higher combinations such as an amide. Apparently ammonia cannot be stored as such in the cells. The rate of intake of ammonia seems to be faster than the intake of nitrate—at least in such plants as the cotton seedling, oats, and buckwheat. Whether ammonia or nitrate is the more suitable form seems to be governed by at least two

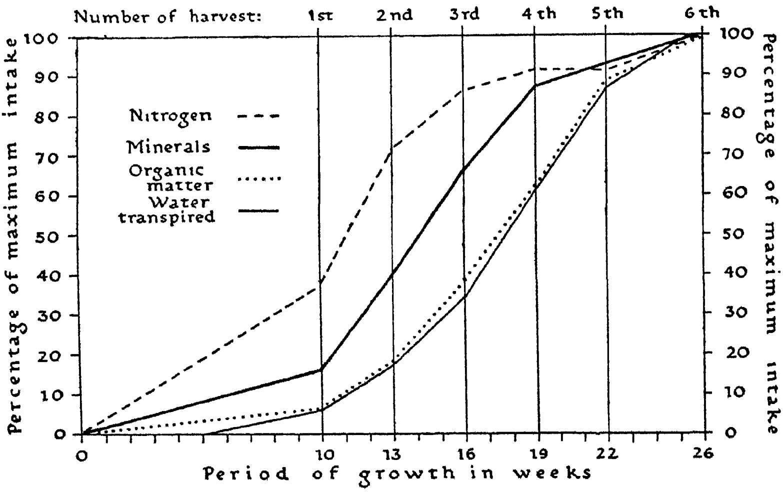


FIG. 149

Graph to show percentage of nitrogen, minerals, organic matter, and transpiration at successive growth stages (harvests) of Barley expressed as percentages of the maximum

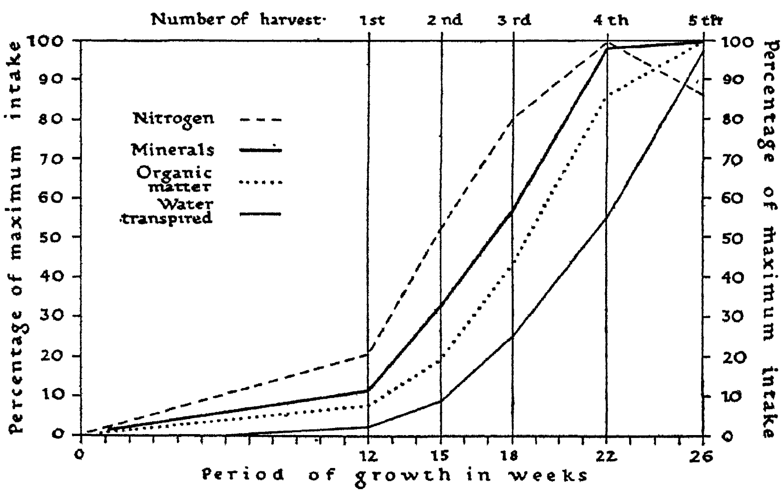


FIG. 150

Graph to show percentage of nitrogen, minerals, organic matter, and transpiration at successive growth stages (harvests) of Wimmera Ryegrass expressed as percentages of the maximum

(*From A. E. V. Richardson, H. C. Trumble, and R. E. Shapter,*

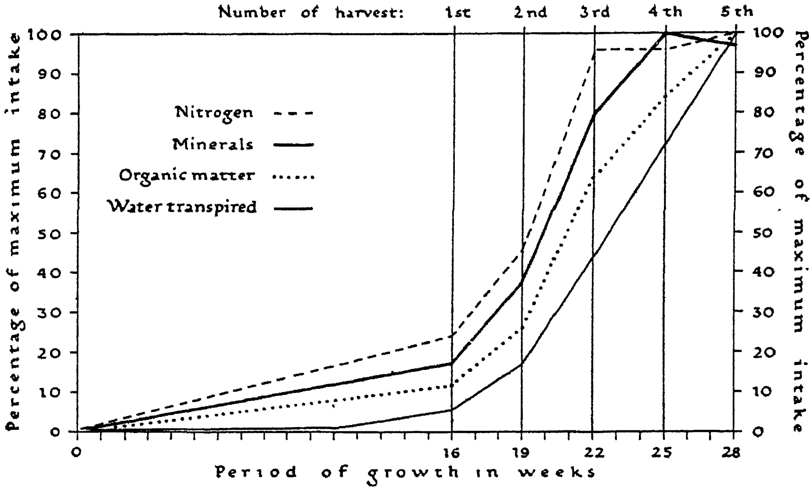


FIG. 151

Graph to show percentage of nitrogen, minerals, organic matter, and transpiration at successive growth stages (harvests) of Subterranean Clover expressed as a percentage of the maximum

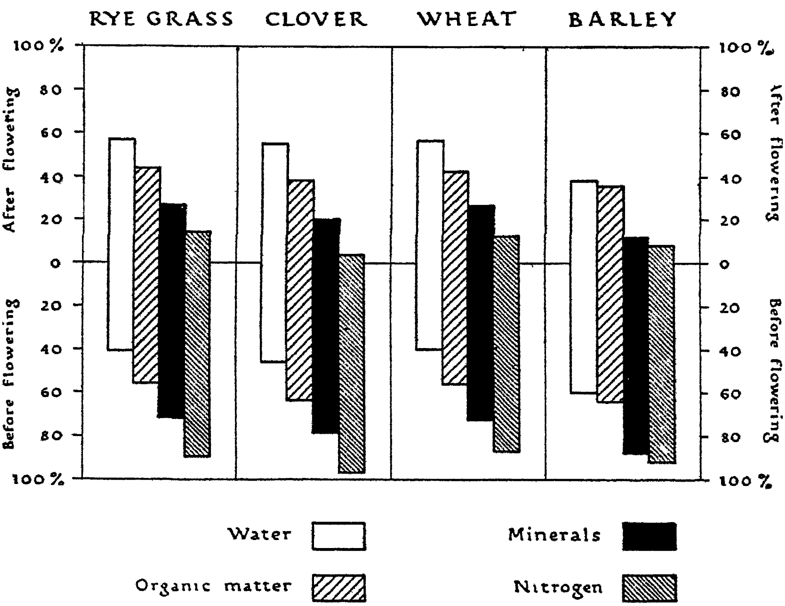


FIG. 152

Graph to show the percentage of total water transpired, organic matter, minerals, and nitrogen assimilated before and after flowering. (Wimmera Ryegrass : Subterranean Clover : Wheat : Barley)

C. S. I. R. Australia Bulletin, 49, 1931)

factors, the nature of the plant and the reaction of the soil. An acid soil favours the use of nitrate. The successful use of nitrite (NO_2) by plants has been reported, but is of little agricultural interest.

The chief use of nitrogen in the plant is in the formation of compounds such as amino-acids, which enter into the molecular structure of the proteins. Since proteins are the basis of protoplasm, reduced nitrogen supply soon shows itself in reduction of protoplasm formation. This puts a restriction on practically all functions, and particularly on new cell formation, so that growth slows and may cease.

(2) *Sulphur*

Sulphur is used by the plant only when offered in the form of a sulphate (SO_4) ; most other forms are toxic or not usable. The sulphur enters into certain amino-acids which are essential in the formation of many proteins. Many plants can maintain apparently normal growth and appearance while suffering from partial lack of sulphur. The tissues are, however, deficient in the element.

A peculiar case of sulphur deficiency occurs in some grassland areas only in spring when growth of the grass is very rapid. The sulphur intake at this time is not sufficient to supply what is necessary for normal protein building, but the plant goes on growing, using such sulphur as it has very economically, or improvising in some other way. A mass of herbage deficient in sulphur is produced. Later in the year, when growth slows down, the sulphur supply is sufficient, so that the maladjustment corrects itself, and normal protein formation follows.

Break in Wool

As wool protein contains much sulphur, sheep grazing in such an area during the spring develop a peculiar characteristic of the wool. When a lock of the wool is sharply pulled, each fibre snaps at the same point, and the broken tuft shows a clean break instead of the irregular break obtained with normal wool. When wool fibres of this type are seen under the microscope an identical part of each fibre is seen to be of reduced diameter. This is the weak point, and is where the break takes place.

Working from known development rates for wool fibre, it appears that the weak part is produced while the sheep is feeding

on the spring flush of grass, which is deficient in sulphur. The condition is remedied by feeding during the deficiency period a " lick " of hydrolized wool, which supplies organic sulphur.

(3) *Selenium*

It will be convenient to discuss one of the non-essential elements here as it is intimately related to sulphur. This is selenium, which is of special interest because it is often absorbed by plants in a quantity sufficient to render them toxic to animals while themselves remaining unaffected. The element is comparatively rare, but traces of its compounds in the soil result in herbage, grain, etc., producing all the symptoms of the dreaded alkali disease when fed to animals. Man, too, is subject to selenium poisoning.

There is no doubt that plants " heap up " selenium, and that the accumulation is due in large part to the metal replacing the sulphur in certain of the amino-acids of the protein molecule.

The process of " heaping up " need not go very far for the plant to become toxic to animals. Rats die when fed on perfectly normal-appearing plants containing 2 or 3 parts per million of selenium. On the other hand, " heaping-up " must go very far before the plants show symptoms. Fifteen parts per million in the plant produces chlorosis, and with greater dosage the leaves and roots develop a pink coloration.

Fortunately selenium and sulphur are antagonistic. Addition of sulphur to the soil substantially reduces the amount of selenium subsequently found in the tissues of the plant. By applications of gypsum, selenium-containing soil can be made to produce crops which are non-toxic to animals.

Selenium-tolerant Plants

Some plants not only tolerate this element so toxic to animals but actually require it for successful growth. *Astragalus racemosus* and *A. pattersonia* are reported as thriving in a medium containing 27 parts of selenium per million. This is about ten times the amount tolerated by wheat or buckwheat. Furthermore, in these plants addition of sulphur to the soil, while resulting in considerable reduction of the selenium content, does not bring it down to a level likely to be tolerated by grazing animals. These species of astragalus are native to the seleniferous areas in America.

Plants which occur naturally on seleniferous soils and nowhere

else are now becoming known. It is expected that delimitation of seleniferous areas by mapping the occurrence and distribution of these "indicator" plants will be comparatively simple, and so eliminate much chemical work on soil analysis.

Selenium as an Insecticide

An interesting development of these discoveries regarding selenium is that crops can be protected from biting or sucking insects if selenium is added to the soil in which the plants grow. Insects die after feeding on the seleniferous juice. This can be made use of without detriment to man or his animals only when the harvested produce is not consumed as food, *e.g.* timber and fibres, or where it is food but not protein, *e.g.* sugar.

A slight exception to this is seen in cacao where the very young plant is subject to attacks from insect pests. The juvenile plantlets are supplied for a short period with selenium, after which they are transplanted to fresh untreated land. By the time the plants are adult and bearing a crop the small amount of this element which protected the small plant is dispersed through a large plant, and the small percentage then present is not toxic in the product.

(4) *Phosphorus*

Phosphorus is of fundamental importance in the economy of the plant, involved as it is in protein formation, as well as in respiration and other functions. The utilization of nitrogen by the plant is interfered with if phosphorus is in deficient supply. This may be due directly to insufficiency of phosphate for the formation of protein. There is evidence, however, that the action lies deeper, for when phosphates are deficient the enzyme responsible for the initial steps in nitrate utilization is either absent or inoperative. Lack of phosphate seems, then, to "bottleneck" the whole of the synthesis in the plant. Mono- and di-saccharides "bank-up," amino and amide nitrogen accumulate, and eventually cell-division slows down and ceases.

The slowing down of cell-division may be a reflex of deficiency of necessary phosphates for protoplasm formation, but it is also known that when phosphorus supply is inadequate the fibres which "pull" the split chromosomes apart in mitosis are not formed. A concomitant of this whole imbalance of cell function is cessation of all phenomena requiring active cell-division, *e.g.*

growth of the axis and branching. This is particularly apparent in cereals where the result is that tillering is depressed. The converse of these effects is seen when phosphate is supplied liberally, for there is then more active branching of the root and shoot, while the plant tends to flower and seed not only earlier but more profusely.

(5) *Calcium*

The predominant rôle of calcium in agriculture is not wholly botanical, but arises from the use of lime as a soil ameliorant and as a reducer of soil acidity. The element, however, is taken into the plant in quite substantial quantities, probably as the metallic ion. In the tissues it neutralizes acids arising from many metabolic activities, and crystals of the calcium salts of oxalic and other organic acids commonly appear in cells.

One of the principal rôles of calcium in the plant seems to be involved in some fine balance with boron, and possibly other elements. What the relationship is still remains obscure. Certainly deficiencies of both boron and calcium are very similar in the symptoms they produce. This is especially so in the failure of normal development in meristematic regions.

Calcium is found in great quantities in leaves, and does not migrate much from an old organ to a young one as the plant develops. Calcium is an essential ingredient of the structure of the cell wall, or at least of the middle lamella.

The Calcium/Phosphorus Ratio

The importance in the diet of animals of adequate quantities of calcium and phosphorus individually, and of the ratio of these to each other, needs no stressing here. The data offered in the general account of salt intake should be again examined from this aspect of the quality of food.

(6) *Potassium*

Potassium in plant nutrition offers something of a paradox in that commonly there is a considerable quantity of potash in the soil with only a small proportion soluble, while in the plant practically the whole of the potassium remains soluble in the cell sap. When a plant tissue is mashed up the potassium may be easily leached out. Despite its appearance in this simple form potassium has fundamental rôles to perform.

Potassium is concerned with the synthesis of carbohydrates, and probably with their translocation. This connection between potassium and carbohydrates is clearly seen in crops which normally accumulate large reserves of starch or sugar. These crops when grown in a deficiency of sunlight produce less reserve food (lower crop yield), but when generously supplied with potash the production is greatly increased. It would appear that potassium can " replace " sunlight.

Potassium is moved out of adult tissues to areas of meristematic activity.

Potash confers on plants some degree of resistance to various diseases. The clovers and their allies, though not " carbohydrate " plants, gain greater benefit from increased potash supplies than do grasses, and hence in pastures with a grass/clover sward addition of potash tends to strengthen clovers rather than the grasses.

(7) *Magnesium*

Magnesium is an essential ingredient for the formation of chlorophyll, and indeed is the only metallic constituent of this all-important green pigment of plants. As the plant passes to final maturity and the leaves change colour, magnesium is largely transferred from the vegetative body to the seed. In the plant another of its functions is connected with its use along with phosphate in the formation of those special proteins which form the cell nucleus (the nucleo-proteins). Magnesium, too, appears to be concerned in oil metabolism.

The amount of magnesium required by the plant is not large and, as has already been mentioned, when too great quantity is available in the soil functional disturbances develop in the plant. See Chapter XIII under Antagonism.

(8) *Iron*

Iron is not an essential element in the sense that the term has so far been used, for only a little is required. Neither is it regarded as a minor element, but occupies an intermediate position in the classification. Iron seems to take no structural part in the plant, yet its presence is essential for the formation of chlorophyll. Though necessary for the formation of chlorophyll, it does not enter into the molecule of that substance.

Iron is not mobile inside the plant. This is easily shown by first growing plants for a time in a solution supplying iron when the shoot is fully green. If the experimental plants are then transferred to a culture medium deficient in iron, the new leaves produced in further growth are white due to a lack of iron in them inhibiting formation of chlorophyll.

Total absence of iron from soils is not so common as total or nearly total non-availability. Thus it is that many soils rich in iron produce plants showing all the symptoms of iron deficiency.

The Minor Elements in Plant Nutrition

(1) *Boron*

Of all the minor elements probably none has received so much attention as boron. It is deficient in quantity in many soils all over the world. Symptoms of disfunction following from apparent boron deficiency seem to be connected with calcium supply, and show fundamentally in reduction or stoppage of activity in the meristematic regions. Further, plants showing symptoms of boron deficiency are found usually in calcareous soils or those which have been heavily limed. Boron does not seem to be necessary to animals, so that the chief interest in this minor nutrient resides in the pathological condition it may set up in the plant.

(2) *Manganese*

Manganese deficiency symptoms, too, are most commonly found in plants growing on soils well supplied with lime. Except at high dilution manganese is toxic to plants, yet when presented in too low a concentration metabolic upsets result. These are definitely connected with lowered efficiency of the respiratory function. Indeed manganese seems to be necessary for the whole oxidation/reduction mechanism. This has been shown in connection with the use of ammonia by plants. Plants offered a nitrogen supply in the form of ammonia compounds are benefited by extremely small additions of manganese to the nutrient medium. This is especially so when the oxygen supply is limited. Additions of manganese seem to benefit the legumes more than other cultivated plants. A sufficiency of manganese in the food is necessary for animals.

(3) *Copper*

Copper has long been known as an element toxic to plants even when present in what may be considered high dilution. For example, one part in 10 million of water is toxic to fresh-water algæ and copper sulphate is commonly used in the elimination of water weeds from tanks, etc.

This element is receiving more and more attention as a minor element. Its increasing importance arises from the fact that copper deficiency causes pathological symptoms in animals as well as in plants.

In the higher plants a modicum of copper is essential, and many soils, often those of a peaty character, fail to provide the very small amount necessary. The addition of $\frac{1}{16}$ to $\frac{1}{8}$ of one part per million in water culture, or about $1\frac{1}{2}$ to 3 lb. of copper per acre, seems to eliminate all trouble in this respect. The element is often supplied in the form of the sulphate or pyrites: the amount of either of these to be sown depends on their copper content.

The mechanism through which the copper acts is not known. That plants deficient in copper are often lacking in chlorophyll is not without importance, for copper deficiency in the diet of infants is often the cause of some of the anæmias that they suffer from. The red pigment of blood and the green pigment of the plant are related in very many respects.

Where copper is in too great supply it has been shown that iron acts as a " depoisoner."

(4) *Zinc*

Deficiency of zinc, too, causes pathological symptoms in the plant. It is thought that the curative action of some fungicidal zinc sprays is more connected with the action of the metal on the physiology of the host that its direct effect on the disease organism.

(5) *Cobalt*

Soils deficient in cobalt produce herbage of normal appearance, but the animals fed on the produce pine and die. The addition of about 2 lb. cobalt chloride per acre eliminates the trouble.

(6) *Molybdenum*

Molybdenum was fairly early shown to be necessary for the nutrition of many fungi, but it is now thought that higher plants use it. Certain soils, typically those lying on the Lower Lias formation in south-east England, contain about 20 to 100 parts per million of this element, and the herbage produced on them may contain about 2 to 3 parts per million. When grazing on such a pasture ruminant animals scour, pine, and eventually die. Such pastures are known as "teart." Clovers seem to absorb more molybdenum than grasses, hence increase of these valuable plants intensifies the bad effect. It would seem that the "availability" of molybdenum is controlled by the acidity of the soil. In neutral or alkaline soils the availability is high; in acid conditions low. Addition of lime to the soil does not render teart pastures healthy, but rather the reverse. Also, the clovers being encouraged by the lime become more prolific, and because of their high molybdenum content they raise the content of the herbage as a whole. There is some evidence that copper may be antagonistic to molybdenum and be useful in treating affected animals or in improving teart pastures.

Other elements affect the plant and through the plant, animals. Enough has been said to elucidate the principles involved, and for fuller details of each case reference should be made to the very voluminous literature which has already grown up.

BOOKS FOR FURTHER READING

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Chapter XV

PRIMARY FOOD SYNTHESIS

Intake of Carbon as Carbon Dioxide

The method by which water and inorganic salts enter the plant having been explained, it falls now to describe the mode of entrance of carbon as the gas, carbon dioxide, the only other ingredient required in food synthesis. Entrance is by gaseous diffusion from the air surrounding the shoot. The greater portion of the gas taken in passes through the stoma pore, though some does pass directly through the cuticle. The main portion of the gas, having passed through the pore into the intercellular spaces of the leaf tissue, rapidly diffuses through them to the cells where

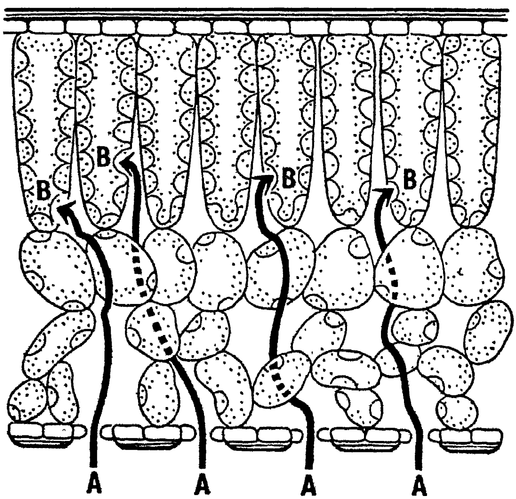


Fig. 153

V.S. of leaf to show track of carbon dioxide molecules when synthesis is active

A Gas-in-gas diffusion through stoma pore and intercellular spaces from outer air to wet cell wall (fast)

B Diffusion as a gas molecule dissolved in water through wall, protoplast to chlorophyll on plastid surface (slow)

active consumption of the carbonic acid gas is going on. This gas-in-gas diffusional movement within the internal atmosphere of the plant is rapid.

The next step, movement into the cells, is slow, for it is a diffusion of a gas in a liquid. The carbon dioxide dissolves in the water dispersion medium of the cell wall and diffuses through it to the green chloroplast, where it is used in the formation of carbohydrate. When the chloroplast is actually engaged in synthesis the concentration of carbon dioxide at its surface is kept very low, and thus the inwardly directed diffusional gradient of the gas is maintained.

As has been seen, this gradient is in two parts at least. The first is a comparatively fast gas-in-gas movement from the air about the plant, through the stoma pore, through the intercellular spaces to the wet cell wall. From the wall to the chloroplastic surface the movement is in watery solution and is comparatively slow.

The methods by which all the necessary raw materials—water, salts, and carbon dioxide—are got into the plant and distributed in the tissues having been dealt with, the actual process of manufacture can be discussed.

The Formation of Carbohydrates

The initial synthesis, fundamental to all others, is the formation of carbohydrates. When water and carbon dioxide meet in presence of chlorophyll adsorbed on a living chloroplast, in light, a series of reactions takes place, and a carbohydrate, probably glucose, is formed. It is an over-simplification to show the equation :

$$6CO_2 + 6H_2O = C_6H_{12}O_6 + 6O_2$$

but finally that is what the process amounts to. Light is absolutely essential for the early steps of this process ; it is the source of the necessary energy. In the equation above this energy intake is not shown. If re-written as :

$$6CO_2 + 6H_2O + 677{\cdot}2 \text{ calories} = C_6H_{12}O_6 + 6O_2$$

a rather more accurate picture is presented. This synthesis, demanding light for its success, is called photosynthesis.

Mechanism of Photosynthesis

There is no doubt that between the initial carbon dioxide plus water and the resulting hexose sugar intermediate products are formed. Numerous theories explaining what takes place have been postulated. What emerges from consideration of these, is that the process proceeds in steps.

The First Stage

The first step is a photo-catalytic reaction in which the chlorophyll acts as a photo-catalyst. An elementary form of carbohydrate, possibly formaldehyde HCHO, is formed at this stage. Its rate depends chiefly on the quality and quantity of the light supply and is little affected, if at all, by temperature.

The Second Stage

The next stage consists in the condensation of this product to a sugar $C_6H_{12}O_6$. This second step is not affected by light and can take place in dark. Plants supplied with a very weak supply of formaldehyde have produced carbohydrate in dark.

The actual mechanism of these reactions is not yet clearly understood, and it is more important to concentrate on how the various environmental factors involved affect the success or rate of the process.

The Principle of Limiting Factors

Working on photosynthesis and realizing that the factors all bore on the rate of the function alternatively and not simultaneously, F. F. Blackman enunciated the Principle of Limiting Factors. This may be stated as, " When a process is conditioned as to its rapidity by a number of separate factors the rate of the process is limited by the pace of the slowest factor."

The author of this principle elucidated the statement given above with an example : Illuminate a leaf with sufficient light to permit it to " fix " 5 c.c. carbon dioxide per hour and no more. If the carbon dioxide supply be restricted to 1 c.c. per hour, only that amount can be formed into carbohydrate. If progressive increments of the carbon dioxide supply be permitted, there will be progressive increments in carbohydrate formation until the supply amounts to 5 c.c. per hour. After that level is passed, no more carbohydrate will be formed in response to increments of

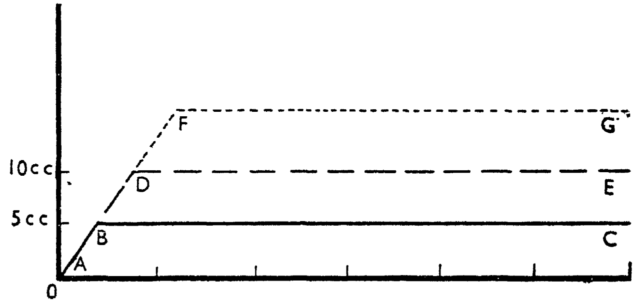


FIG. 154

The Principle of Limiting Factors

(From F. F. Blackman, Ann. Bot. xix, 1905)

the gas supply. At the stage where the carbon dioxide supply is less than 5 c.c. per hour, it is the limiting factor. After the 5 c.c. level has been passed light becomes the limiting factor. The sequence of these events may be shown graphically as in Fig. 154. The graph AB shows the effect of gradual increments of carbon dioxide up to 5 c.c. At B the light supply becomes limiting and there is no further increment in the rate of photosynthesis as shown by the graph BC. The continuation of the graph BD shows the effect of doubling the light supply followed by increments of carbon dioxide. The line DF represents the results obtained following a similar set of increments of both factors.

The two factors are seen to be alternate and not simultaneous in their action. Increments in the limiting factor, *and that one only*, will result in increase in the rate of the function.

The principle has been criticized from many points of view, but as experimental methods improve it seems likely that its validity will be fully established. The principle is not only of use in dealing with photosynthesis, but can be used with advantage by investigators after truth in many diverse fields.

Measurement of Photosynthesis

A number of methods of measuring photosynthesis have been devised. Some of these depend on ascertaining the amount of carbohydrate in a leaf or part of one, or in a portion of shoot such as a twig, at the beginning and end of an experimental period. Estimation of the carbohydrate demands that the plant material

be killed. All of these methods therefore require samples of the plant material to be drawn for the first analysis and then other samples to be drawn for subsequent analyses. This introduces possibilities of error when the experimental plant material is not absolutely uniform.

Other methods rely on measuring the intake of carbon dioxide and/or the output of oxygen by a given unit over a known time. Measurement of carbon dioxide intake is probably the simplest method. For this, air of known carbon dioxide content is allowed to flow over a leaf for a given time and the amount of carbon dioxide still left in it is measured. The difference between the amount of the gas in the inflow and outflow is ascribed to photosynthesis: the product of respiration is ignored.

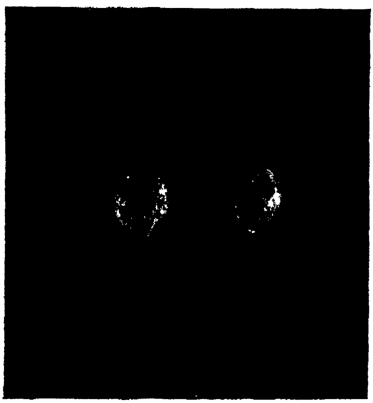
Plate 62 shows an apparatus designed for this purpose. A leaf still attached to the plant is enclosed in a cellophane envelope into which a glass tube enters. This tube is connected through an absorption tower to a suction pump. When the suction is "on" atmospheric air enters through the space at the mouth of the bag between the petiole and the tube. After passing over the leaf the air is carried by the suction to the absorption tower where the carbon dioxide is taken out and evaluated. The figure so obtained after a known time is compared with the figure obtained from a similar control chamber containing no leaf. The difference between the two amounts of carbon dioxide is ascribed to the photosynthetic activity of the leaf.

A glass cup chamber sealed on the under surface of another leaf and used in the same way provides figures of a similar character though pertaining to photosynthesis over a restricted area which obtains its carbon dioxide through the lower epidermis only.

Temperature and Photosynthesis

Examining the various factors bearing on photosynthesis, first mention may be made of temperature. It may be said that, considering green plants as a whole, photosynthesis is possible within a very wide range of temperature—from well below freezing point to quite a high point. In crop plants of the temperate regions, however, the rate of the function is probably only of real significance from somewhere approaching 5° C. to somewhere just under 35° C. Above this maximum the photosynthesis mechanism fails progressively with time. The actual effective

MISTLETOE ON MOUNTAIN ASH (ROWAN TREE)
This partial parasite is green and photosynthesizes



SEED OF DODDER
The plant is devoid of chlorophyll and is totally parasitic. (See Colour Plate No. XIV)

SYMBIOSIS
Tubercles or nodules on root of legume caused by the "attack" of nitrogen-fixing bacteria

ROOT HAIRS HIGHLY MAGNIFIED

Left The bacterium enters at the hair tip and in ection passes down *Right* The hairs after infection become contorted

(*Copyright. Rothamsted Experimental Station*)

range of temperature within which the organism functions normally depends on the kind of plant.

Between about 12° C. and 20° C. the process obeys the Van 't Hoff rule with a Q_{10} of 1·87. In other words, provided no other factor becomes limiting, the process nearly doubles in rate for every increase in temperature of 10° C.

Carbon Dioxide Supply and Photosynthesis

When CO_2 supply is the limiting factor the rate is proportional to the supply. There is a top limit to this however, because, when too concentrated, the gas has a narcotic effect on the living protoplasm.

Light Supply and Photosynthesis

As regards light there are three aspects to be considered. These are the intensity, the wave-length (colour), and the length of time for which the light is incident.

(1) *Intensity of Light*

The rate is proportional to the intensity, subject to an upper limit above which the light has a disabling effect on protoplasm. Some plants in the tropics suffer from insolation, and require to be shaded from the fiercest rays of the sun.

(2) *Wave-Length*

Much of the earlier work on colour was vitiated by the fact that plants were tested under different colour-filters, and the different amounts of energy transmitted through each was not equalized or allowed for.

There is now evidence that the "most efficient" light is in the red region of the spectrum, with another useful part in the blue region. Only about 20 per cent. of the whole spectrum of sunlight is fully efficient in photosynthesis.

(3) *Period*

As regards time it seems clear that the plant can photosynthesize more per unit of time if illuminated for a series of comparatively short periods than for the same total time but in longer periods. The protoplast would seem to tire. Fig. 155 shows the relationship between photosynthesis and variations in external factors

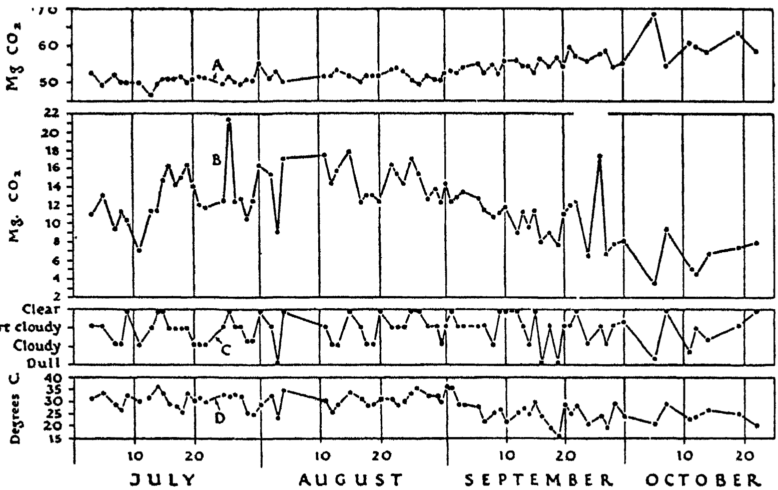


FIG. 155

Photosynthesis in Apple

Average carbon dioxide assimilation by a leaf in cellophane envelope (as chamber) during four hour determinations between 8 a.m. and 2 p.m., from July to October

A Fluctuations in carbon dioxide supply (milligrams per litre of air)

B Assimilation of carbon dioxide in milligrams per hour per 100 sq. cm. leaf

C Relative light intensity

D Mean temperature

(*From Heinicke and Hoffman, Bull. 577, Cornell Univ. Ag. Exp. Stn., 1933*)

under almost completely natural conditions. These results were obtained from a leaf in a cellophane envelope of an apparatus similar to that shown in Plate 62.

Internal Factors affecting Photosynthesis

(1) Of all the factors affecting the rate of photosynthesis, probably the state and amount of living protoplasm is the one of greatest importance. Age of the plant is significant in this regard. It has been shown that if the photosynthetic ability per unit of leaf area of a young sunflower be taken as 100, the efficiency of a similar area of a leaf on a half-grown plant is only 40, while that of a fully adult plant is down to 30.

(2) The quantity of chlorophyll in the leaf may become the limiting factor. When the amount of the green colour is considerably reduced, as in a variegated leaf, the rate of function falls.

The Locus of Photosynthetic Activity

From what has been said it will be clear that any part of the plant containing chlorophyll adsorbed on a living protoplast, supplied with carbon dioxide, and exposed to light, is capable of forming carbohydrates, but that the leaf is the main site of the work. As photosynthesis proceeds, and the sugar content of the cells rises, a number of other processes affecting the fate of this material come into action. First, the sugar may be moved away to areas of lower sugar content. In many plants, if this movement away is not so quick as to equal the rate of production, the sugar content of the cell sap rises above the equilibrium point of the amylytic enzymes, and carbohydrates of more complex nature—polysaccharides such as starch—are formed. These appear as small solid grains, and constitute an insoluble temporary "reserve" in the leaf. In the dark, or when for any other reason production of elementary forms ceases, the movement away continues. Under these circumstances the sugar concentration falls below the equilibrium point, and the temporary reserves are hydrolysed back to soluble forms. The products of this hydrolysis, too, are transported away, and the temporary reserves disappear. The starch grains formed in this way when photosynthesis is active do not constitute a reserve in the strict sense of that term. As they are insoluble, their formation, as concentration of hexose rises, prevents an undue concentration of osmotically active material accumulating in the cells of the leaf tissue.

A second fate for the products of synthesis arises from the fact that the protoplasm in the leaf cells is engaged in other work for which light is not an effective source of energy. A quota of the sugar produced is consumed to provide this energy.

Thirdly, saccharides are required as the basis of the synthesis of the more complex classes of food substances such as amino-acids and so on.

Locus of Protein Synthesis

Probably the locus of much of the synthesis of these more complex types containing nitrogen is in the leaf. Either ammonia or nitrate nitrogen brought from the root seems to be used by plants for the synthesis. Thus in the leaf the inorganic salts brought up by the transpiration stream meet carbohydrate, and synthesis is possible. The condensation of amino-acids and other forms of " brick " to proteins goes on in the leaf.

Locus of Oil Formation

In the formation of oils, too, carbohydrate is necessary, but it is doubtful if this synthesis is predominant in the leaf. Fats do not easily migrate as such in the plant, and it seems rather more likely that synthesis occurs in the cells where the oil droplets are commonly found. The picture would in this case be one of delivery of carbohydrates from the locus of their formation to the tissue capable of forming oil. At the oil synthesising end glycerol is formed from carbohydrates as well as organic (fatty) acids. The acids then react with the glycerol to yield the glycerides of the fatty acids, that is, oils.

Few facts are available regarding the formation of such other classes of organic compound as alkaloids, glucosides, tannins, and so forth, which are often found in the plant.

Chemosynthesis

Photosynthesis provides for all the primary fixation of carbon in the world except for an extremely small amount produced by non-green plants belonging to the group Bacteria. Agricultural interest in these latter cases arises not so much from the fixation of carbon, but from the nature of the by-product. Soil bacteria of the type referred to, use energy derived from the oxidation of inorganic substances to build food from carbon dioxide and water.

Such a synthesis is known as chemosynthesis, not photosynthesis, because chemical energy is used instead of light energy.

Examples of Chemosynthesis

An example of chemosynthesis is provided by members of the genus *Nitrosomonas*, which oxidize ammonia to a nitrite and manufacture carbohydrate. Similarly, members of the genus *Nitrobacter* by the oxidation of nitrite to nitrate, obtain the energy to form foodstuffs. The usefulness of these by-products (nitrite and nitrate) are obvious when it is remembered that many of the higher plants use nitrate almost exclusively for their nitrogen supply. There are many other cases where different bacteria oxidize such substances as sulphuretted hydrogen to sulphuric acid, ferrous oxide to ferric oxide, and so obtain energy to produce carbohydrate.

Median longitudinal section of maize fruit (low magnification)

The region stained pink is the embryo and the brown region the food reserve or endosperm. The outer covering is the transparent fruit-wall fused with the testa. The scar of attachment to the parent is at the base and the remains of the stigma on the left-hand hump at the top

The embryo of maize (higher magnification)

On the left the plumule points upwards, the radicle downwards —this is the embryonical axis. The shield-like structure on the right is the scutellum (cotyledon) used in the absorption of the endosperm

COLOUR PLATE XIV DODDER—A PLANT PARASITE

The dodder plant has twined round the stem of the host and sunk haustoria into the underlying tissues. Death of the host follows abstraction of its food by the parasite

These bacteria use only carbon dioxide as a source of carbon and make no use of soluble carbonates. Light does not assist the work, if it does not actually inhibit it. Neither does a supply of soluble organic matter assist the organism.

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Chapter XVI

IRREGULAR NUTRITION

Just as after completing water intake a digression in the main discussion was made to consider water relationships, and after salt intake to review the effects of different salts, so it is proposed now, having completed the study of regular nutrition, to note some of the cases of "irregular nutrition."

Parasites and Saprophytes

Under irregular nutrition reference will be made to those plants which obtain their nutriment in whole or in part from a source other than the direct method of carbon-dioxide intake and primary synthesis.

There is an almost perfect gradation of types from the wholly independent green plant to those completely dependent for all food on an outside source. These cases should be regarded as evolutionary variations in advance of the regular type, though "morally" they may appear retrograde. This, because all of them depend on another plant to provide that which they require. When the accessory food supply is of dead organic material, the plant is a saprophyte. When part of a living organism is consumed the plant is a parasite. The living organism on which a parasite feeds is called its "host."

The degree of dependence on the accessory food supply may be partial or total, and so there are recognized partial saprophytes, partial parasites, and total saprophytes and total parasites.

The fungi, lowly non-green plants are all either parasitic or saprophytic, except for the chemosynthetic types. They will be considered now only in a few special cases, for the main interest at this point will be in connection with parasitic and saprophytic flowering plants.

Partial Parasites

Perhaps the simplest forms are those when the parasite at first sight appears as a normal plant, fully green and living with its roots below soil level. Some of these plants have their roots sunk not in the soil but in the roots of their neighbours.

Eyebright, yellow rattle, lousewort, cow-wheat, and other denizens of grassland are all examples of partial parasites with at least part of their roots fixed in the roots of a host, usually a grass. These partially parasitic plants draw from the host the salts and water they require. They are all fully green and apparently quite capable of being self-supporting apart from intake of water and salts. Whenever plants are in close propinquity, as in the tangle of roots of a green sward, there is danger that by physical contact ability to " rob " may evolve. A clearer case of semi-parasitism is seen in mistletoe, which grows up in the branches of a tree and has no direct connection with the soil. This plant draws only salts and water from the xylem of the host. It is a partial parasite, and because it rests on another plant, so obtaining a better place in the light, it is called an epiphyte.

Loranthus, a partially parasitic epiphyte of the tropics, is closely related to mistletoe. It not only plunges sucking organs (haustoria) into the host, but creeps along externally, repeating the process as it goes.

Total Parasites

In the agriculture of temperate regions two totally parasitic flowering plants are of interest, namely, dodder and broomrape.

Dodder

Dodder is a non-green flowering plant related to bindweed or convolvulus. It twines round the host plant in an irregular helix, and throws out long side stems to catch on to nearby plants which may be still uninfected. As dodder depends on a host for the whole of its food, its evolution has resulted in the disappearance of leaves or their reduction to very small scales. So far has this process of reduction gone that there are now no leaves in the embryo. The root (radicle) in the embryo, too, is rudimentary, and at germination appears only as a mucilagenous pad, which merely serves to anchor the plant to the surface of the soil until organic contact is made between the leafless stem and a host. The thread-like shoot axis produced on germination grows irregularly, first on one side and then on another, and as a result the stem tip sways about, describing an irregular circle. When the swaying stem makes contact with the stem or other part of a suitable host, the parasite grows round the part and then pulls tight. An organ (*haustorium*), resembling a highly modified

adventitious root system, is produced by the dodder, and this plunges into the tissues of the host. Soon organic contact between the haustorial-conducting tract on the one hand, and the phloem and xylem of the host on the other, is completed. Food passes from the one plant to the other.

The parasite now grows quickly, and by repeated branching soon spreads from host plant to host plant over a whole area, smothering it in yellowish-red, thin, leafless, hair-like stems. The parasite in course of time flowers very freely, and produces a very large number of small seeds. Colour Plate XIV.

Profuse seed production is a characteristic of a total parasite. This high rate of reproduction counteracts the risk of no seed ever being placed near to a host. This risk of not making physical contact with a suitable host is increased in dodder by the fact that there are many kinds of the plant, and each can attack only one kind of host and perhaps some of its closest relatives.

This means, in other words, that each kind of dodder is more or less specific to a particular host. For example, it is believed that the dodder which attacks flax cannot attack any other plant. The clover dodder seems to prefer red clover, though it may not be completely restricted in this regard, and may attack alsike. The different kinds of dodder are rather difficult to tell one from the other, hence the evidence for specificity is not too clear.

Prevention and Eradication of Dodder

The seed of dodder is often introduced on to the farm as an impurity in consignments of seeds used for sowing. This is recognized in the legislation controlling the seed trade (see p. 214). In cases when the precise identification of the seed is in doubt (after machining, many different kinds of seeds may resemble those of dodder) the specimens should be put to germinate. If cotyledons develop, the seed is not that of dodder.

This parasite germinates in the field only under moist and warm conditions, hence it occurs in Britain only in the early autumn, and its distribution is confined to the more southern areas. Once dodder appears in a field (it is usually in clover) the infected area should be cut over close to the ground, and all the herbage removed. A fire of straw should be lit on the soil surface. It is of first importance that no part of a dodder plant be left alive, as it will act as a propagant and restart the infestation.

Broomrape

Broomrape is also a total parasite of crop plants which attacks the roots of specific hosts. The very small seeds, produced in myriads, germinate below ground, and the seedling attaches itself to the roots of a suitable host. After haustorial connection has been made between the conducting tissue of host and parasite, a brown tuberous body forms. After feeding on the host for some time a yellowish-brown axis comes above ground bearing yellowish-brown scale-like leaves. There is no chlorophyll in the plant. Eventually the axis produces purplish flowers, and later very many small, dust-like seeds. Colour Plate xv.

Various kinds of broomrape attack a very wide variety of hosts. The clovers and many plants related to them are commonly parasitized in this way.

Both broomrape and dodder should be eliminated from a crop with great care. They both reduce the yield of crop considerably, and dodder especially may kill the host by its depredations.

Irregular Nutrition in Supplement of Nitrogen Supply

Many cases of irregular food habit arise from the almost universal shortage of available nitrogen from which plants often suffer. The insectivorous plants which attract and kill insects in modified leaves do so in order to supplement their nitrogen supply. These, while of great botanical interest, hardly affect the agriculturist. It may be merely noted that they absorb the simple compounds derived from the rotted or digested corpses of the insects.

Symbiosis

Symbiosis describes a conjoint life of two or more different organisms, the relationship being more or less beneficial to both the partners or symbionts.

Many cases of this are known, especially in connection with the obtaining of supplementary nitrogen. One of these is seen in practically any pea or bean plant or any of their relatives. If one of these leguminous plants is carefully dug up, small wart-like nodules will be found on the roots. These are formed by proliferation of the plant's root tissues in response to the stimulus given by the attack of a bacterium. Inside each nodule are cavities filled with the bacteria. These micro-organisms have the

faculty of using energy derived from carbohydrates to "fix" gaseous atmospheric nitrogen. That is to say, they can form protein from nitrogen derived from the air, while carbohydrates obtained from the legume (host) provide the energy required.

The host evidently obtains nitrogen by absorbing the bacteria or the products of dead and decayed bacteria. In short, in the normal condition the bacterium and the host obtain a mutual benefit from this association and so constitute a case of mutualism or symbiosis.

There are a number of strains or races of the nodule bacterium, each of these being capable of "infecting" only one, or a small range of very closely related kinds of legume. In short, each kind of leguminous crop plant is specific to its particular bacterium. The appropriate race of bacterium must be in the soil before the young plant can become infected.

Where a kind of legume is to be grown in a field for the first time, it is often useful to inoculate or infect the land with the appropriate strain of bacterium. This can often be done most easily by obtaining soil from a field which has carried a well-infected crop of the same plant. Cultures of different strains of bacteria may be obtained from laboratories and applied to the soil along with the seed or in other ways.

How the Nodule Forms

Given that the proper bacterium is present in the soil, infection of the host takes place through the root hairs. The furthest tip of a hair is attacked, and in favourable conditions a small gelatinous mass of the bacteria develops soon thereafter. This is the zooglœa stage. The root hair then becomes contorted and deformed. The organism has now gained entry, and passes through the cortex to a point close to the stele. Cell division of the host is stimulated, the bacteria multiply rapidly, and the typical nodule forms.

Physiological Balance between Bacterium and Legume

The leguminous plant can live quite successfully without the bacteria if it is supplied with inorganic nitrogenous salts. In the absence of the micro-organism the plant fails if supplied with atmospheric nitrogen only.

This does not end the matter, for there seems to be a most

delicate physiological balance between the two partners or symbionts. If there is an ample supply of nitrate or ammonia nitrogen available in the soil, the bacteria are incapable of penetrating the root hair, and so infection is reduced or completely precluded. Furthermore, any addition of manurial nitrogen to an already infected crop reduces subsequent nodule growth or development. On the other hand, the addition of a readily available carbohydrate such as glucose or sucrose along with the nitrogenous manure mitigates the effect. The addition of inorganic combined nitrogen alone upsets the carbon/nitrogen ratio, and this affects the relationship between the two plants.

The balance between the symbionts can be upset in other ways. For example, anything which reduces the vegetative vigour of the host, and reduces the free flow of carbohydrates to the nodule, tips the scale adversely for the host, and the bacterium gains the upper hand, when it behaves like a disease-causing parasite.

Soil Conditions and Legume Symbiosis

The best conditions for successful symbiosis between the legumes and the nodule bacterium seem to be those which are conducive to healthy growth of the host. In particular the soil should not be either acid or badly aerated. In good conditions for symbiosis the host plant benefits directly from the accessory nitrogen supply, but so do its non-legume neighbours. Nitrogen accumulates in the soil either by leakage from the intact nodules or from their rotted remains following death or harvest of the host plant, and becomes available to other plants.

Symbiosis Between a Flowering Plant and a Fungus

In addition to the symbiotic relationship between a bacterium and a leguminous plant, more advanced fungi often enter into similar coalitions with non-legumes. The kind of fungus varies with different hosts, and the hosts are representative of very diverse kinds of plants.

Fungal symbionts on roots are known as mycorrhiza. There are two forms. With some hosts the mycorrhizal filaments are confined to the exterior of the root; in other hosts the fungus inhabits cells of the sub-surface tissues. The first is known as ectotrophic mycorrhiza, the second as endotrophic mycorrhiza.

Ectotrophic Mycorrhiza

In the ectotrophic type the affected root is wrapped in a felt-like covering of fungus. This " weft " prevents direct contact between the root and the soil, and all intake from the soil to the plant must pass through the fungus. The fungus extracts nutrients from the decaying organic matter of the soil, which is rarely rich in readily available carbohydrates. The host plant supplies this lack, but draws nitrogenous material from the fungus.

Endotrophic Mycorrhiza

In endotrophic mycorrhiza, the fungal filaments lie inside the cells of the host root, chiefly in those of the cortex. The functional relationship between the two organisms is somewhat the same as in the ectotrophic condition, for the fungus acts as an intermediary between the plant and the soil. The only difference is that the host of an endotrophic mycorrhiza certainly benefits by " digesting " some of the fungus.

In both of these types of symbiosis the relationship is probably one of a defensive mechanism in the host countering the attack of a would-be parasite. A state of balance between defence and attack is attained, and mutual benefit happens to accrue.

In some cases the mycorrhizal fungus has been isolated and identified. Many of these have been found to be types which under different circumstances are capable of acting as virulent parasites.

The relationship is of importance in forestry and to some extent in horticulture, but the incidence of mycorrhizal symbiosis seems of very limited occurrence in agricultural crop plants.

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COLOUR PLATE XV
BROOM-RAPE—A PLANT PARASITE

The roots of the parasite have become attached to the roots of a clover plant. The host will die from loss of food

COLOUR PLATE XVI

"BURN" IN GRASSES NOT WELL GRAZED

A cocksfoot plant in early spring. Leaves not grazed in the previous year are brown and inedible

CHAPTER XVII

RESPIRATION

RESPIRATION in plants is sometimes described as the reverse of photosynthesis, and as the taking in of oxygen and the giving out of carbon dioxide. Though this is true, the statement ignores the real significance of the function, which is the release of energy by the breaking down of various compounds in the plant.

It is a step by step process, each step in the reduction of the complexity of a molecule releases a moiety of energy locked up in it. It is true that commonly the end product of respiration is carbon dioxide, and it is true that where such is the case the rate of respiration is easily measured by the amount of oxygen consumed and/or the volume of carbon dioxide given out.

RESPIRATORY QUOTIENT

When both the intake of oxygen and the output of carbon dioxide are measured, it is found that the ratio between the two quantities depends on the nature of the compounds used by the plant as the source (respirable substrate) of the energy released. The ratio is called the respiratory quotient.

$$\frac{\text{Volume of } CO_2 \text{ exhaled}}{\text{Volume of } O_2 \text{ taken in}} = \text{Respiratory Quotient (R.Q.)}$$

When glucose is being consumed the simple picture may be presented as

$$C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O + 677{\cdot}2 \text{ cals.}$$

and the respiratory quotient is $\frac{6}{6}$ or 1. There is very little deviation from this if another of the hexose sugars is used, and the equation is simply the reverse of the photosynthesis equation.

When an oil provides the material for respiration the amount of oxygen required is greater, for in the fat molecule there is a greater proportion of hydrogen and carbon to oxygen. This can be shown simply as

$$C_{54}H_{104}O_6 + 77O_2 = 54CO_2 + 52H_2O + \text{approx. } 8{,}000 \text{ cals.}$$

The respiratory quotient is here $\frac{54}{77}$ or approximately $0{\cdot}7$.

The Consumption of Fats

In the plant the first step in the process of the respiration of a fat is the transformation of the oil to a carbohydrate. This requires a considerable volume of oxygen, with no output of carbon dioxide. In studying the respiration of a fat-containing organ, say in the germination of an oil seed, if only the oxygen intake and the carbon dioxide output are recorded, these provide a summation of the two processes involved, namely, transformation of the fat to saccharide, and then the degradation and respiration of the carbohydrate. In such a seed the dry weight would rise in the earlier phases of the dual process. This is due to the combination of oxygen with the oil molecule to form a greater mass of carbohydrate.

One point of special importance in agricultural practice is that all these respiratory processes involve the production of water as an end product. This is called *metabolic water*.

Proteins occupy an intermediate position between carbohydrates and fats. When they provide the respirable material the respiratory quotient is 0·81.

Respiratory quotients greater than 1 may be obtained when some compounds such as organic acids are respired.

The Energy Value of Different Foods

As has been said, the end products of respiration are not of great biological interest; it is the energy released which is of prime importance. The energy output from each type of food has been calculated. With a R.Q. of 0·7 it is found that 4,686 calories are released per litre of O_2 absorbed. With an R.Q. of 0·81, 4,813 calories of energy are released per litre of oxygen, while 5,047 calories are made available under similar circumstances when the R.Q. is 1. With intermediate values for the R.Q., intermediate values for the energy released are obtained.

Respiration in Practical Agriculture

There are very many points of botanical interest associated with the study of respiration. For example, there are the details of the mechanism involved, and the intermediate compounds produced, between, say, the initial reaction of the hexose molecule and the final stage, production of carbon dioxide, but it is rare

for the agriculturist to be involved with these matters. It is usually in connection with stored foodstuffs that agriculture has to meet problems in respiration. Enormous quantities of potential energy may be confined in limited space—in a grain silo, in a pile of bagged grain, or in a stack of a newly harvested straw crop. If respiration is active in these there will be spoilage of food, and the danger that much of the energy released may be in the form of heat. " Heating " of such a mass may go to such an extreme that, given the right circumstances, spontaneous combustion (fire) may develop.

Heating : Oxygen Supply

Most of these storage difficulties arise when the material is closely packed, and hence the supply of oxygen is low. In such circumstances the plant may use oxygen derived intra-molecularly. Then there is output of carbon dioxide, with little or no intake of oxygen. In most cases in practice there is some oxygen present, and some cells of the tissues respire in the normal way, aerobically, and others by intra-molecular adjustment—that is, anaerobically.

Aerobic and anaerobic respiration go on in close juxtaposition when the supply of atmospheric oxygen is only sufficient to supply part of the demand. Always in respiration (aerobic or anaerobic), part of the energy is released as heat (a waste of energy on the plant's part apparently). In any situation where this heat is rapidly dissipated no harm results, but in a compact bulk the heat is confined, and the temperature of the mass rises. Up to a point every increase in temperature results in an increase in the rate of respiration, hence the product of activity of the function increases that function still further. Between, say, 0° C. and 30° C. the temperature coefficient Q_{10} for respiration is rather higher than 2 but less than 2·5.

Heating : Water Content

In practice the factor chiefly affecting the respiration rate involved in the production of heat is not temperature but water content. At a low water content the protoplasm of the living material is dormant, and respiration, like any other function, remains more or less quiescent. If the water content of the protoplasm in the tissues is above a certain point respiration is active. This produces more water (metabolic water) and more heat, both of which further raise the rate of respiration.

The relationship between water content and rate of respiration

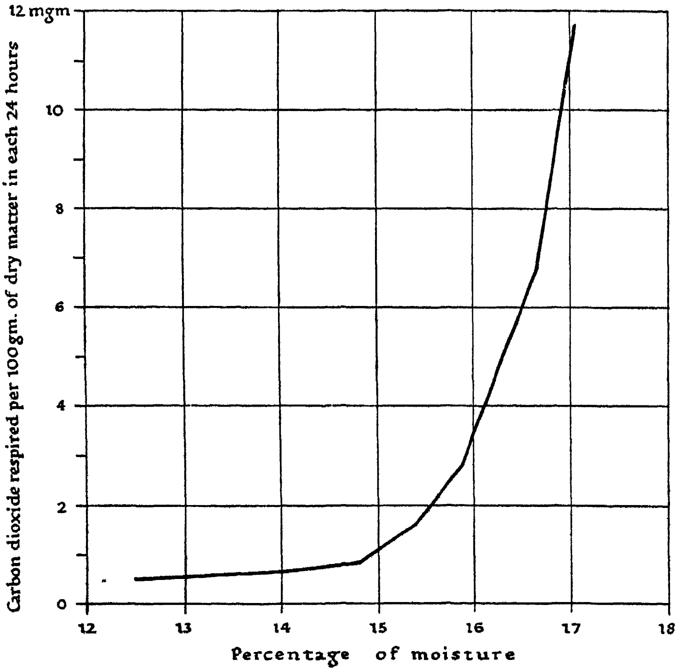

FIG. 156

Respiration of Wheat

The relationship between rate of function and moisture content

(Note steep rise at about 14·75 of moisture)

(From C. H. Bailey, Jour. Ag. Res. 12 (11), 1918)

is therefore important, for there is a water content below which respiration rate is low, and above which the rate of the function rises steeply. Fig. 156 brings this point out very clearly. This *critical water content* is being worked out for all the various grains which are commonly stored in bulk. For wheat it would seem to be about 14·75 per cent., and round this figure for other cereal grains. The water below the critical point is very strongly held by the colloids present as bound water. Above the critical point the colloids are satisfied, and the additional water is loosely held.

It is to be noted that a mass of seeds, etc., with a water content below the critical point, if stored in a humid atmosphere, may attract water vapour to themselves from the air, and so gain sufficient moisture to start the process off. The water produced by respiration (metabolic water) still further increases the hydration of the remaining protoplasm.

T.S. root of Lime Tree showing weft of fungus on the outside (Ectotrophic Mycorrhiza)

Root of Lime Tree showing white wefts of fungus on many roots (Ectotrophic Mycorrhiza)

Root of Philesia showing fungus in the cortical cells (Endotrophic Mycorrhiza)

Induced root formation in Gooseberry hardwood cutting after treatment with naphthalene acetic acid 1/20,000 for 24 hours

L.S. of the cutting in illustration above to show origin of the rootlet (Naphthalene acetic acid induces thick roots; those produced by indolyl compounds are more fibrous)

(From unpublished photos by M. A. H. Tincker, by permission of Roy. Hort. Soc.)

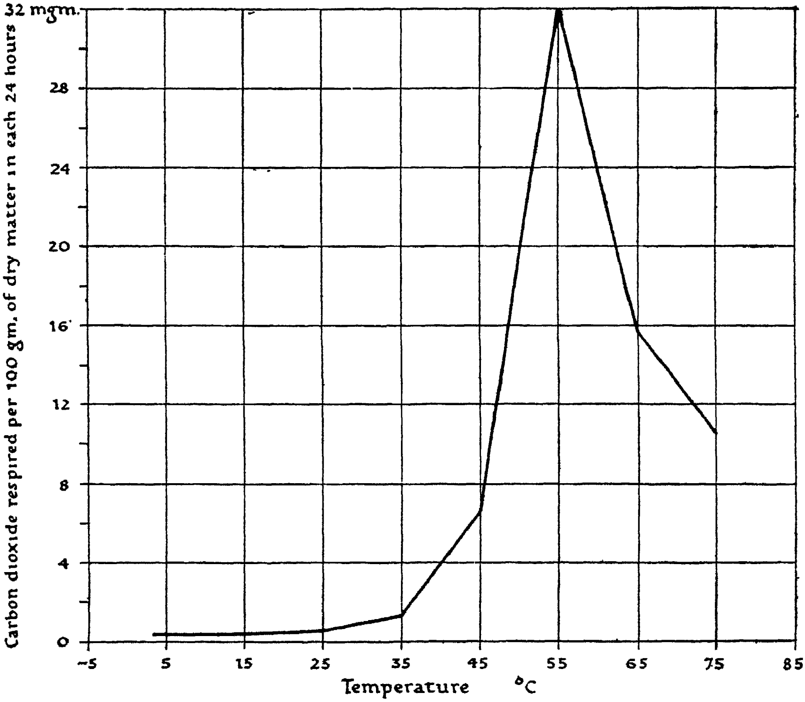

FIG. 157

Respiration of Wheat

The relationship between rate of function and temperature

(*From C. H. Bailey, Jour. Ag. Res.*, *12* (*12*), *1918*)

Prevention and Cure of Heating

Heating of grain bulks or stacks, etc., may be prevented by ensuring that all material when placed in position is below the critical water content. Kilning of the material may be necessary with many products. Once heating has started the action may be arrested by reducing the water content of the mass as quickly as possible to below the critical point. This may be done by blowing *warm* dry air through it, opening the mass so as to expose it to a dry atmosphere, and so on. Care has to be taken that when the mass is opened up it is not already so hot, due to anaerobic respiration, as to go on fire when free oxygen is admitted. If material capable of active respiration (not dead) has to be put into bulk or stacked in a

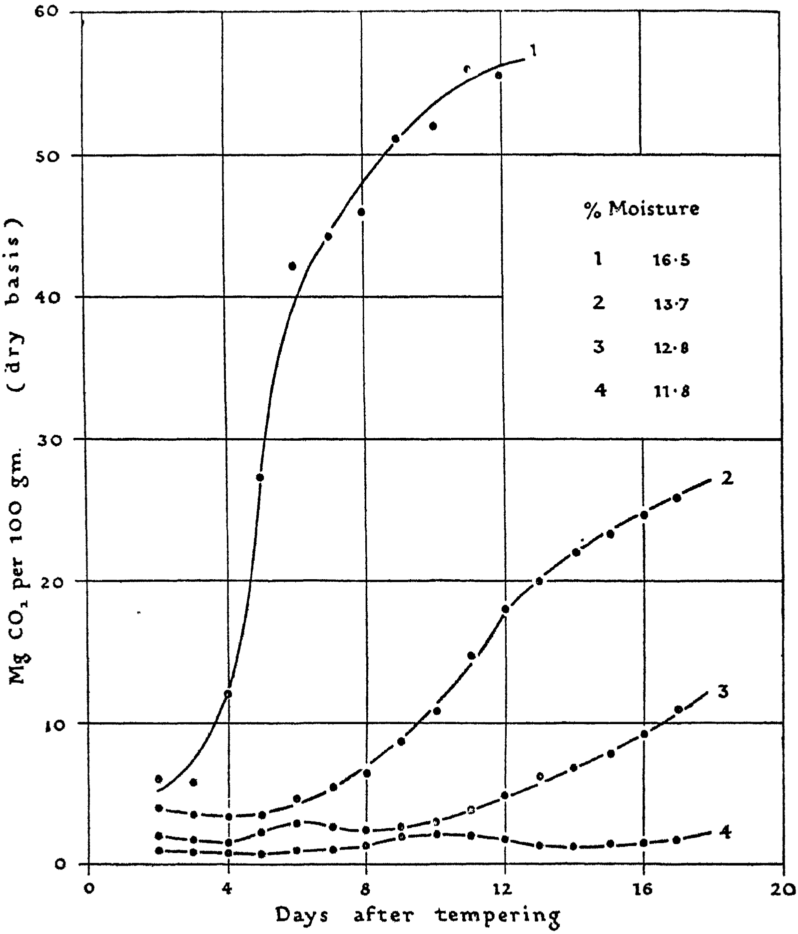

FIG. 158

Respiration in Flax Seed

The effect of wetting (tempering) dry grain

(*From R. K. Lamour and Co-workers, Canadian Jour. Res., F22 : 9-18, 1944*)

"wet" condition, every precaution should be taken to ensure that there is free circulation of dry air through the mass, so that heat is conducted off and the water content progressively reduced.

Not all heating of stacks, etc., is to be ascribed entirely to respiration of the material itself; bacteria living on the food, by their respiration, produce heat.

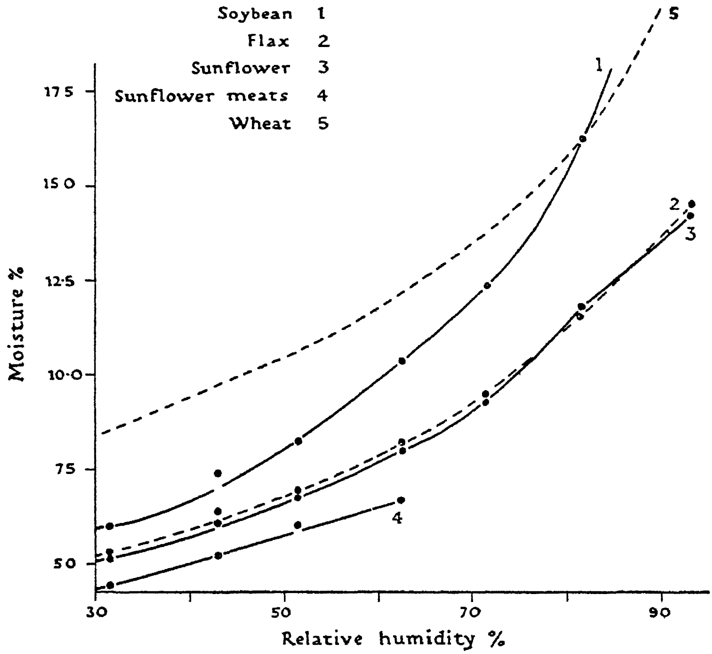

FIG. 159

Dry seeds may absorb moisture from the air. Water content of seeds stored in air differing in relative humidity

(*From R. K. Lamour and Co-workers, Canadian Jour. Res., F22 : 1–8, 1944*)

THE MECHANISM OF RESPIRATION

The mechanism of respiration is essentially one of enzyme catalysis. Not all the steps are oxidations ; some involve inter-molecular transfers of hydrogen—dehydrogenation. The molecule giving up the hydrogen is known as the hydrogen donator, and the molecule receiving it, the hydrogen acceptor. An enzyme catalysing such reaction is known as a dehydrogenase, while an enzyme catalysing an oxidation belongs to the oxidase group.

The intermediate compounds produced in the degradation of even a simple hexose are various, and it seems clear that in the breakdown of glucose to carbon dioxide and water, phosphate enters into some steps.

Fermentation

One aspect of respiration is seen when the yeast plant is living in a sugar solution of suitable concentration. The last moiety of

energy is not extracted by the yeast from the sugar, for the process stops when the substrate is reduced as far as alcohol. Yeast contains an enzyme, zymase, which catalyses the reaction.

$$C_6H_{12}O_6 \longrightarrow 2C_2H_5OH + 2CO_2 + 25 \text{ calories.}$$

The reaction does not go on indefinitely, for once the concentration of alcohol reaches about 15 per cent., the yeast ceases active function.

End-products other than alcohol are obtained when other organisms are employed and different substrates supplied, but all are aspects of energy release in which the process stops short of totality. The whole of the energy is not extracted from the substrate, and of course the quota of carbon dioxide produced is low or in some types of reaction nil.

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Chapter XVIII

TRANSLOCATION OF FOOD

The movement of food materials from place to place within the plant has been referred to in the text more than once, and this will be considered in rather more detail. Controversy still goes on as to the fundamental mechanisms involved, but a number of important points have been settled.

Slow and Fast Movement

There are two aspects of translocation, slow movement from cell to cell by simple diffusion, and fast movement from one part of the plant to another along the conducting tract of the phloem. Both these movements are on a diffusional pattern ; that is, from an area of higher concentration to an area of lower concentration, or, as it has been put, from a " source " to a " sink." Any part of the plant with a comparatively high concentration of a small enough food molecule in solution behaves as a source. It may be an area of primary synthesis, such as the leaf, or an area where stores previously deposited are being hydrolysed. A sink is constituted by any part where the concentration of the same diffusible unit is low, and may be an area of active consumption such as a meristem, or an area engaged in very active respiration. A storage organ in process of building up reserves for the future, by forming compounds of larger molecular size and of an insoluble character, acts as a sink. So too do developing fruits and seeds. In these areas the diffusing particle is either condensed to insoluble forms or destroyed by respiration.

The Mobile Particle

The molecules actually moved must be comparatively small, hence the more complex food molecules are hydrolysed to simpler forms prior to movement. Starch is broken down to a monosaccharide, protein to amino-acids or other degradation products of approximately similar size. Each kind of molecule moves in the plant along its own concentration gradient. This means,

for example, that any one amino-acid moves in a direction and at a rate irrespective of the movement of another amino-acid. Further, a mass of protein already formed in an area does not affect the continued movement of amino-acids into that area, for not only are the protein molecules too big for movement but they are not an amino-acid, and hence do not affect the amino-acid concentration gradient. Thus it is possible to see amino-acid continuing to stream into an area comparatively rich in protein from an area quite poor in the more complex class of substance.

So, too, carbohydrate may move from an area comparatively poor in *total* carbohydrates to an area rich in *total* carbohydrates, provided the equilibrium point of the enzyme systems or relative consumption/production rates in the two areas concerned are at the one end maintaining the carbohydrate mostly as a sugar, and at the other end predominantly as a polysaccharide. Condensation or consumption at the sink end, and hydrolysis or production at the source, maintain the gradient of the diffusing particles.

Multiple Sources

There may be more than one source and more than one sink. Multiplicity of sources, say a number of leaves at different levels on a shoot and all of them actively synthesising, leads to no confusion, for each individual pours its quota into the channel of transport according to its capacity.

Multiple Sinks

Multiplicity of sinks, as, for example, when a number of growing points and actively developing flowers are all on one plant, may lead to difficulty in the interpretation of experimental results, but this does not confuse the general picture.

In this regard the conception of steepness of gradient can be a help. Just as water falls down a steep hill more easily and more quickly than down a gentle slope, so does a diffusing molecule pass down gradients of different steepness. Hence any organ maintaining by condensation or consumption the lowest concentration of the diffusing metabolite receives the most of that metabolite.

When supplies in the general channel of conduction are sufficient to meet completely the demands of all sinks, all sinks are supplied. When supplies in the conducting channel become

limited, however, the steepest gradient is filled to capacity while the shallower gradients receive little or nothing. Thus, where demands are high and supplies limited there is competition between sinks, and the sink which maintains the lowest concentration of the mobile metabolite is supplied while the others starve. As will be shown later in Chapter XIX, inter-sink competition for a limited supply of food has a profound effect on the relative growth and development of different parts of a plant.

The Mode of Action

These points being established, it is possible to construct an image of what takes place. Take carbohydrate first. Primary synthesis or the hydrolysis of temporary reserves in the leaf maintains a high pressure of monosaccharide in the cells there. A diffusional drift of this fairly mobile particle takes place through the mesophyll, from cell to cell, towards the phloem. This movement is comparatively slow. On entering the sieve-tube the hexose condenses to form disaccharide. This has two effects. First, it maintains the sink of the through-the-leaf gradient of monosaccharide at a low level at the phloem, and secondly, it maintains a "head" of sucrose at the top of the sieve-tube. Hexose passes from cell to cell and sucrose moves in the phloem. The movement of sucrose in the tubes is very fast, and though the mechanism is known to be diffusional in pattern, the reason for the high rate of speed is not understood. Suffice it to say that the sucrose moves at a rate approximating to that of a gas molecule of the same size diffusing in air.

Arriving at the sink end of the phloem in the tissues there the sucrose is converted by condensation to a diffusionally inert form such as starch or is consumed, and the sink there is maintained. The "insulation" of the sieve-tubes for sucrose is not complete. Some sucrose leaks out all along its length, hence there are lateral gradients running out from the tubes to living cells in the axial cortex, medullary rays, etc.

The movement of nitrogenous material is on the same pattern—movement of a small molecule into the sieve-tubes and then fast distribution. Fats may be translocated as glycerine and fatty acids, but more research is required before this can be substantiated or fully explained.

It is seen that for carbohydrate and organic nitrogen, at

least, the movement may be up or down the axis, the direction taken depending only on the location of sources and sinks. For example, in the developing seedling of broad bean, the cotyledons inserted midway between the two axial meristems are the source, while the root-tip and shoot-tip are sinks. Hence food metabolites " diffuse " down the phloem of the cotyledonary petiole into the axial phloem, and from there the stream splits, one part going down to the radicle and the other part up to the plumule.

BOOKS FOR FURTHER READING

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CURTIS, O. F. *The Translocation of Solutes in Plants.* (McGraw-Hill Book Co. Inc., New York, 1935)

MASON, T. G., and PHILIS, E. "The Migration of Solutes." (*The Botanical Review, 3 (2), 1937*)

CHAPTER XIX

GROWTH AND DEVELOPMENT

The Balance of Production and Consumption

THE metabolism of the plant has been described in so far as it has an application for the agricultural botanist. There is a long train of events, processes, and reactions which lead from simple raw materials to a seemingly bewildering variety of organic products. Yet the story is simple. The high energy dry matter in the plant is increased by synthesis. Opposed to this upbuilding or synthesis there is the story of energy release, one of degradation and consumption of the dry matter by respiration.

Under normal circumstances upbuilding goes on faster than breaking down, and after a time the surplus of production over expenditure, though possibly diverted to a number of different uses, leaves a "credit balance" of dry matter in the plant. (Terms common in finance and banking are often used in this way, *e.g.* the "net credit balance" of dry matter. Care has to be used in adopting such terminology, as the analogies may not be perfect.) The balance resulting from metabolism may be stored for future use by the plant. It may be placed in a seed for the endowment of the next generation. It may be used immediately for strengthening an existing organ or forming a new one. All these fates or uses have a different investment value or potential.

Often growth and development should be looked upon as separate functions. Growth is defined as a permanent, irreversible increase in size, volume or mass; development as an increase in complexity. Thus a shoot going on steadily with vegetative growth repeating node, internode, node internode, may be said to grow well, but as there is no new type of structure produced there is no increase of complexity, and it is said to grow but not to develop.

With time the plant may be induced to produce new types of structure or highly modified forms of an old structure with vastly different functions, as, for example, flowers, fruits, and seeds. It is then said to develop. It is difficult at the moment to envisage

development without increase in size, and therefore to divorce completely the two functions.

At some times it is convenient to consider them as separate ; at other times it simplifies discussion to take them as one expression.

The Dependence of Growth on Metabolism

The study of growth and development is complicated by the fact that they are both affected by the same external factors (light, temperature, etc.) as metabolism. Metabolism is the provider of the materials for growth. Increase of mass or complexity in a plant possessing no significant reserves is based directly on metabolism. Without its immediate products, growth and development are not possible. Hence if each external factor affects both metabolism and growth differently as to their rates, then measurement of growth may provide figures which are due more to the vagaries of metabolism than to those of growth itself.

Effect of Heredity

The genetical factors internal to the plant, those underlying abilities, disabilities, and special characteristics which help to make it what it is, are transmitted from parent to offspring, and may affect metabolic function. Rarely do they do so in the spectacular way that they influence growth and development. For example, there is an obvious difference in development between an early flowering variety and a late one, and again there is a spectacular difference in growth between a tall and a dwarf variety, but there is no spectacular or obvious difference between their metabolisms. The study of growth and development of a plant thus demands some knowledge of its genetical constitution, as well as of the course of its metabolism during the period of observation.

Measurement of Growth

An approach to the study of growth may be made by considering examples of the ways by which it may be measured.

(1) *Increase in Population.* With plants which reproduce quickly by simple means, merely enumerating the increase in numbers in given time under different conditions may be of use. For example, in a culture of the unicellular yeast plant which increases in

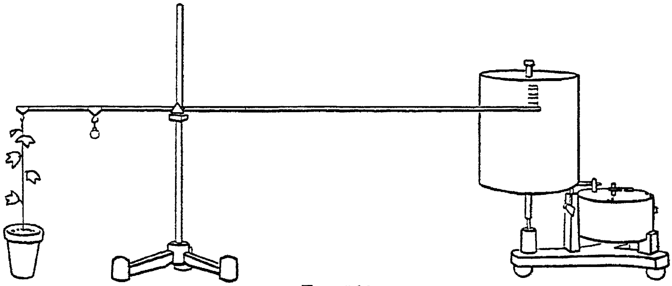


FIG. 160

An Auxanometer

As the plant grows the angle of the lever alters, and a pin point traces a line on the smoked drum. The drum is moved on its axis periodically by the clock. This causes the pin to draw horizontal lines at definite intervals of time

number by cell division, or the multicellular water-plant duckweed which increases by simple fission, "counting heads" at appropriate intervals yields valuable figures.

(2) *Increase in Length.*—A simple method for use on a crop plant is to measure the increase in length of an axial structure such as a stem. This may be done by direct methods, as by the use of a "yard-stick" of appropriate scale. If the increments are small some method of magnification may be necessary, as by the use of a lever. This is commonly adopted for demonstration purposes, and a recording drum is usually incorporated in the apparatus so that the movements of the lever are traced on a smoked drum. Other marks due to the activity of a clock appear on the drum to indicate intervals of time.

Various disabilities attach to the use of a lever which, though made of the lightest material, must impose a traction on the axis. The use of a small mirror reflecting a beam of light provides a method whereby the weight moved by the plant's growth may be reduced to a minimum, while the length of the lever (reflected beam) may be as great as optical conditions permit.

Various ingenious devices have been developed to reduce the disabilities of the lever principle applied to measurement of plant growth, but none seem to apply well in practice.

(3) *Increase in Dry Weight.*—The method which has proved of greatest practical utility considers as growth the "net credit balance" accruing from metabolism. Measurements are made of the dry weight increase of the plant over a given time. This has disadvantages. The chief of these is that the experimental

plants have to be killed to make the necessary analyses. This difficulty is met by using in the experiment a large number of plants as alike in genetical constitution as possible. At the beginning of the experiment a number (sample) of the plants are taken for the initial estimation of dry weight. Then from time to time a number of the remainder are sampled out and subjected to analyses.

So long as the plants are reasonably alike genetically, and sufficient are used for each analysis to satisfy statistical considerations of sampling, the method provides valuable results.

The Unit to be Measured

Many of the methods described have implied that the whole plant is the unit measured. This may not be what is required nor valid. Consider a potato tuber growing in a dark cellar. The shoots produced from the " eyes " grow ; they increase in length ; they increase in dry weight ; they satisfy completely the strict definition of growth. Yet the plant as a whole does not. As the shoots increase the tissues respire, and the total dry weight of shoots plus tuber falls.

An even more striking case is seen in a dodder seedling. This totally parasitic plant itself cannot form dry matter. If the seedling fails to meet a host the substance of the tissues at the base of the axis is dissolved away, leaving only cell walls, and the products are translocated to the axial apex. The plant progressively moves forward, growing at the " head " and dying at the " tail." The length of axis left alive decreases, for respiration slowly consumes the dry matter of this almost reserveless seedling. The case is obviously one of growth, but its accommodation within the strict definition is difficult.

Theories regarding Growth

A number of theories regarding growth have developed from the kind of data obtained from the measurement of " dry weight " increase.

One of these theories or concepts of growth describes the function in banker's terminology, and the process is likened to money put out at compound interest. The initial dry weight of the seed is regarded as capital, the rate of increase in dry weight as the rate of interest.

If W_1 be the initial dry weight,

W_2 the dry weight after time t,

r the rate of interest and e the base of natural logarithms (2·718),

$$\text{then } W_2 = W_1 e^{rt}.$$

Plant growth over short periods and in special cases may be fitted into this formula. But the rate r is not stable ; it falls with time. This fall in the " earning power " of the " capital " is due to two causes. In the first place, all dry matter present in the plant is not primarily engaged in producing more dry matter, and the proportion of such " non-earning " material (fibre, vessels, and dead cells) increases with age. Dead cells such as sclerenchyma, while necessary to the life of the plant, do not contribute directly to the synthesis of more dry matter. Secondly, as was shown under photosynthesis, the efficiency of the protoplasm falls off as the plant ages. So that even in a plant which produces no dead cells the rate r will fall in time.

The idea of growth as connected with compound interest is therefore only of theoretical value.

Another theory draws an analogy between growth and an autocatalytic reaction, *i.e.* one where a product of the reaction catalyses the activity, and thus as the reaction proceeds the amount of catalyst increases and the rate rises with it. Many experiments on growth provide data supporting this view, and indeed the statement is often made that growth *is* an autocatalitic reaction. This view of growth may be stated briefly as : the more growth the plant makes the more it can make. This is hardly true if growth be measured in terms of dry matter increase, because the balance between respiration and photosynthesis does not remain constant. For example, at germination and at spore formation plants consume more by respiration than at other stages of development. This is well brought out by data shown in Fig. 161.

In this generalized curve which applies to maize—an annual plant—the initial curve A–B is the period before the photosynthetic organs are able to counterbalance the loss of dry weight due to respiration.

The curve B–C corresponds with the phase of morphological development during which the leaf area per unit of dry weight increases to a maximum. The curve C–F covers the remainder of the life cycle of the plant.

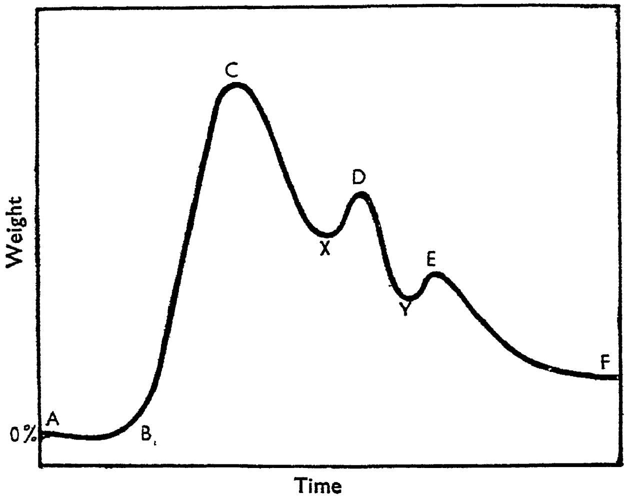


Fig. 161

Generalized form of growth rate curve for maize

This is the weekly percentage increase in dry weight plotted against time

(*From Briggs, Kidd, and West, Ann. App. Biol. 7, 1920*)

The subsiduary maxima of D and E coincide with the appearance of male and female flowers respectively. The minima at X and Y which precede these maxima correspond to the early stages of flower development and are probably due to increased respiration during these periods.

The "Grand Period" of Growth

No matter what individual unit may be studied, if the growth rate under constant conditions is plotted against time, the form of the curve is S-shaped. This is the curve of what is called the "grand period of growth," or the period through which the plant or plant member exhibits its sequence of growth rates.

In studying growth rates of a root system a series of S curves, one following the other, have been obtained. The first S represents the growth of the branches of primary origin, the second that of the branches of secondary origin, and so on. The initial depression of each S is occasioned by the high respiration which accompanies the formation of a branch initial.

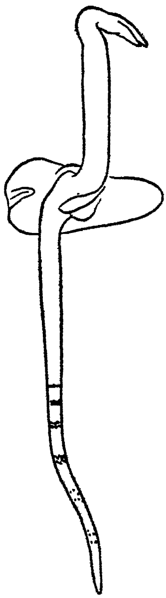


FIG. 162

A young root marked originally at equal intervals after growth shows the marks in the active zone spaced out

Growth is Localized

Growth does not take place uniformly throughout an organ, but is localized in definite regions.

In a root, growth is typically in a region commencing a little way behind the tip and extending backwards for perhaps 10 mm. In a shoot, elongation is localized in the upper parts of the upper internodes; the nodes grow very little and soon stop.

A peculiar case of growth at a node is seen, however, when a grass plant is placed in a horizontal position. By this treatment a quiescent meristem, located in the node, is stimulated to grow on the lower side. The lower aspect of the node elongates and the stem turns upwards. A knee forms at the node. This reaction is commonly seen where a straw crop has become lodged or laid by stress of weather.

Growth in leaves is most active in the region nearest to the stem.

Even in a single growing region growth rate is not equal throughout. This is easily proved by making marks at equal distances along a growing axis, say that of a young root. Some time after marking, where growth has progressed, the marks will be seen to have altered. Some will be wider apart; some will have remained at the distance they were originally placed.

A statement regarding growth in length demands three pieces of evidence: the time interval over which the observations are made; the length of the active region; and the increase in length recorded. With these the elongation in time can be expressed as a percentage of the length of the whole growing region. This provides a reasonable basis of comparison between plants of quite different growth habit.

The Phases of Growth

Growth in length of an axis or similar structure is more than mere addition of tissue on tissue or cell upon cell. The whole process of elongation may be considered as separable into three stages or phases. First, there is the production of new cells by mitotic division. Then follows a phase where each cell increases in size and becomes vacuolated. The third phase is one in which the cells differentiate and alter in character for some special function.

The first phase (cell division) takes place at growing points, and, as we have already learned, the axial primary meristems form from an embryo or from a previously existing meristem.

After mutilation of an axis growing points may be reconstituted. A case of restitution of a growing point is seen in the field when the tips of the axis of a tap-rooted plant such as turnip is damaged, and two growing points develop. " Fanged " roots in a root crop are often produced in this way.

In many plants if the whole root is cut off transversely and the base of the stem laid bare, as in a stem-cutting, repair of the damage may take place by the production of adventitious roots. The production of a special tissue is often a prerequisite of such regeneration of a growing point. This tissue, called " callus," forms from a ring of meristematic parenchyma cells at the exposed cambium ring, and then slowly spreads over the whole wound surface. The exposed surface of the callus mass may become suberized over. By differentiation of cells of the callus the new organ is produced.

Hormones or Telemorphic Substances

The regeneration of new growing points and the control of existing growing points so that the various parts are kept in an organized harmonious whole is undoubtedly conditioned by internal messengers or hormones. The name telemorphic substance has been coined for these compounds which induce an effect at a distance from the point at which they originate. The effect produced by such a substance is referred to as a telemorphic effect. A hormone or telemorphic substance is a chemical compound synthesized in one tissue and transferred to another, where it induces a characteristic reaction. Thus a stimulus applied to one part of a plant is " perceived " there, and results in an altera-

ESCALLONIA CUTTINGS

(A) Water only. (B) Alpha naphthalene acetic acid 4/10,000. (C) Beta indolyl acetic acid 4/10,000. (Note that in B and C the hormone supply has been slightly too strong and killed the stems at their base)

EUCRYPHIA GLUTINOSA

(A) Control (untreated). (B) Alpha naphthalene acetic acid 1/30,000 for 24 hours. (C) Beta indolyl butyric acid 1/60,000 for 24 hours

(From M. A. H. Tincker, J. Roy. Hort. Soc. 61 (1936) and 63 (1938))

Methoxone inhibits formation of roots of Rape seedlings growing on Agar

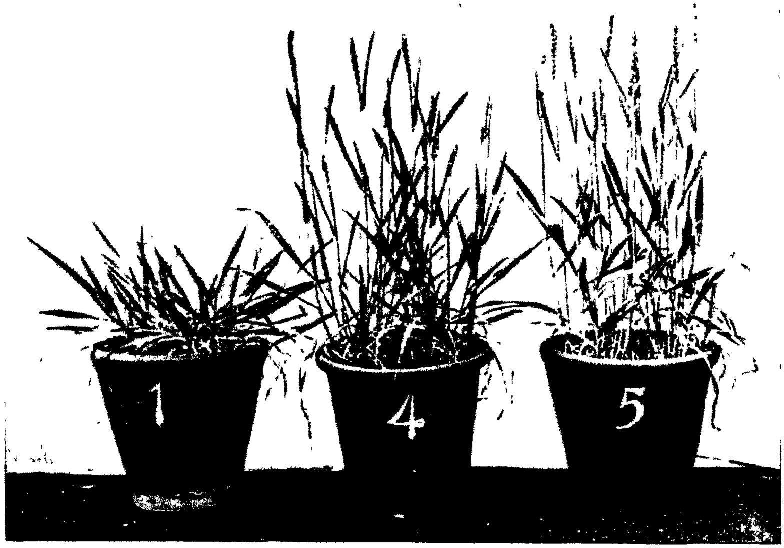
A plant of Charlock three days after spraying with methoxone. It is contorted, later it will die

(*Copyright, Messrs. Plant Protection Ltd.*)

PLATE 69 LIGHT AND GROWTH

Left A plant illuminated from the right bends that way *Right* A plant stored in the dark produces shoots with long internodes, small leaves, and no green colour—they are etiolated

Two varieties of Wheat sown in February, No. 6 Rajah (Australian) and No. 8 Hen Gymro (old Welsh winter var.) grown under short days. No. 1 Red Marvel grown in 16-hour days for comparison



Three varieties of Wheat grown under 16-hour days; sown in February, photographed in July

(From M. A. H. Tincker, Annals of Applied Biology 19 (3), 1932)

tion of hormone output. Alteration in the quantity of this hormone arriving at another part affects that part, and changes appear in its growth and development. For example, if a shoot be illuminated laterally from one side only it will respond by greater growth on the darker side, with the result that the stem becomes concave on the illuminated side. It is said to bend towards the light. It is at the tip of the shoot that perception of the light difference is made, but it is the region some way below which shows the growth response. Unilateral disbalance of hormone supply to the level capable of active growth produces a different growth rate on the two sides.

Root-promoting Hormones

The hormones of greatest interest to the farmer and gardener are those which cause root development to be stimulated. The amount of these present even in a stimulated plant is small and their extraction difficult. A whole range of synthetic substances have been made, identical with or having the same effect as the natural hormone. These compounds can be prepared by the chemist, and are now available in quantity. Examples of those which are commonly employed in practice are β indole-acetic acid and phenyl-acetic acid. They are used at very low concentration, either in watery solution or as " ointments " or pastes made up in lanolin. The most usual method is as solutions.

Application of these and other growth-promoting substances affects not so much phase one of growth (production of new cells) as phase two, which is the expansion of cells, vacuolization, and the formation of intercellular spaces. Little is known of how the hormone substance exerts its influence. Appropriate hormones are useful in all cases where it is desired to speed up root development. This is especially so in taking cuttings for propagation, for if the roots form quickly there is less chance of death amongst the propagants. It is to be noted that in those plants resistant to propagation by the usual methods (the kinds the gardener says are " difficult to strike ") the use of root-promoting substance has no great effect. The use of hormones in propagation seems to lie mainly in their ability to speed up rooting. Different kinds of plant require different concentration of the chemical. If the concentration used is too low no effect is produced, while if above optimal the plant is affected adversely and may easily be killed.

Another use of the application of these substances is in delaying abscission, that is, the cutting-off of an organ or part by the plant. Leaf-fall and fruit-drop are aspects of abscission. For example, spraying an apple tree with alpha-naphthalene acetic acid at a strength of 10 parts per million of water a little before picking time will cause to be retained on the tree, fruit which would otherwise drop off immature and unripe. The retention of such fruit increases the total picked at harvest and more than pays for the cost of spraying.

The Use of Hormones as Herbicides

The application of growth-regulating substances in concentrations much above optimal produces malformation, contortion of the various organs, and death of tissues. For example, application of lanolin paste containing 2 per cent. of indol-acetic acid resulted in death of the tissues near the treated region. As many of these telemorphic substances act more vigorously on some plants than on others, the vagaries of their disabling effect in higher concentrations renders them useful as differential weed-killers, killing some plants but not others.

A full understanding of hormone action when it becomes available will give the grower an increased command over growth and development of the plant, but it must be noted that in this regard nutrition exerts a predominating influence. The balance between vegetative activity, reproduction, and fruiting is probably more profoundly affected by the character and quantity of food supply to the meristems than by any other single factor.

The Effect of Food Supply

This aspect has been most clearly demonstrated in the tomato. Here a series of plants were treated each with different levels of nitrogen supply but none with excess. The appearance of the plants after a time made it clear that while additions of nitrogen promoted vegetative growth (leaf and stem), it also promoted flower and fruit development.

The position was clarified when it was recognized that it is not the absolute amount of nitrogen available which conditions the balance between vegetative vigour and reproduction activity, but the ratio of usable nitrogenous compounds to the amount of carbohydrate present.

This and much other evidence has led to the concept of the carbohydrate/nitrogen balance. The C/N ratio which produces most successful vegetative growth is probably not the same as that required for full fertility and eventual fruitfulness. This ratio may be manipulated in practice in a number of ways. The amount of inorganic nitrogen supplied to the roots may be raised or lowered by appropriate manuring or top-dressing, and so the amount inside the plant controlled. Increased nitrogen increases the number of leaves produced, and these in course of time produce more carbohydrate. Left to itself the plant will thus tend to return to an appropriate balance. On the other hand, the ratio is altered by reduction of the carbohydrate when the plant is stripped of its leaves, or when its reserves are taken away by an appropriate system of pruning.

Competition between Different Organs

Another aspect of nutrition affecting the character and the amount of meristematic growth is seen when the ideas outlined under translocation of foodstuffs are brought into the discussion. In a plant bearing fruit, flowers, flower buds, and vegetative meristems (shoots and root apices) these may all be regarded as "sinks" drawing from the total bulk of available food in the plant. As long as there is sufficient food of every type to supply adequately each of these consuming regions no untoward symptoms appear. It is known, however, that these "sinks," while they all make a heavy demand on the supply of nitrogenous compounds, are not all of equal "pulling power." As soon as the gross supply of nitrogenous food in the plant falls below a level sufficient to supply all, the weaker members starve. If the supply is not then increased the next weaker members starve. In short, when a number of organs or "sinks" are in competition for a limited amount of food, the weaker members will starve.

From this concept of sinks competing for a limited food supply comes the explanation of the fact that, in the event of such competition, elongation of root and stem is often seen to stop on a fruiting plant. If the deficiency is allowed to develop, and the supply of nitrogenous compounds is not added to, flower and flower-bud development are next curtailed or stopped.

The axial meristems are weaker sinks than the flower. The most powerful sink is the fruit. If when nitrogen deficiency

becomes acute the developing fruits are cut off, their competition for the amount of nitrogenous food present is eliminated; the other sinks then obtain a quota and again become active. They will remain active until a new set of fruits develop and the earlier position is again established. Addition of very readily available nitrogen to the root when fruits are developing, by increasing the supply in the plant, often permits of a supply to all sinks.

The principles it is desired to emphasize are, first, that the activity of one part of the plant can have a considerable reaction on another part, and this through a purely metabolic or nutritional mechanism. Secondly, that nitrogen supply does not necessarily stimulate leaf production at the expense of fruitfulness, that vegetative growth is not necessarily antagonistic to yield of fruits, but rather that the two are interdependent. Thirdly, that while an early plenitude of nitrogen stimulates leaf production, this "over-production" of leaf will be counterbalanced later. The additional leaves, if the plant is given time, increase the total production of carbohydrate, and this will readjust the ratio. This later statement is emphasized by observations made on carbohydrate-storing crops (potatoes and beets). These plants, if manured with nitrogen much above usual, will give an increased yield of carbohydrates per acre, provided the growing season is long enough. If the plants are not cut down by frost or disease the extra leafage produced by the early over-plus of nitrogen will synthesise more carbohydrate.

External Factors affecting Growth

The effect on growth of each of the more important external factors may now be considered.

Temperature and Growth

Growth is accelerated by increasing temperature. With cotton and many other plants this holds good for a range of temperature extending from above 0° C. to about 27° C. or 29° C. Above this level a factor inside the plant (internal factor) commences action and growth rate falls off. The Van 't Hoff coefficient (Q_{10}) within the middle of the temperature range has a value of between 2–3.

Four cardinal points may be recognized in connection with

temperature, and these apply to all plants. They are : (*a*) the minimum temperature below which growth is not possible; (*b*) the maximum temperature above which growth ceases; (*c*) the maximum rate temperature; and (*d*) the optimum temperature. The optimum temperature is that one which produces the fastest rate of growth and from which there is no falling off in time. In other words, the optimum is the highest temperature which does not affect the internal factor. The maximum rate temperature is that which stimulates the plant to its fastest growth even for a short period, but where the rate falls owing to the adverse effect of the temperature on the state of the plant (internal factor). Temperature, along with other factors, bears significantly on the onset of reproduction, a developmental rather than a growth expression.

Light and Growth

Light affects the growth of plants. The light supply may vary in any of three ways. In intensity, in quality (wave-length or colour), and in the length of the period for which it is incident.

Intensity

As regards intensity it may be said that shoots in total darkness develop extremely long internodes. At low intensities elongation of the stem axis is roughly inversely proportional to the intensity of the light. Above a certain intensity of light further increments have no effect on growth. A plant growing in dark or reduced light, therefore, has a typical appearance : long internodes, small leaves, and little or no green colour. It is said to be etiolated. When plants are partially etiolated they are said to be " drawn," or pulled up towards the light. There is evidence that a shoot grown in dark develops an endodermis with a true Casparian strip. The elongation of the internodes is ascribed to the action of this tissue in preventing lateral diffusion of foodstuffs out of the phloem, and so diverting the whole supply to the apical meristem. The plant seems to " appreciate " exposure to even quite short periods of light if they are of sufficient intensity, and shows a response by increased development of the leaf lamina and shortening of the internodes.

The effect of light intensity on branching is important. Up to a point the greater the intensity of the light the plant receives

the more it will branch. In agricultural practice the quantity of light reaching each plant is controlled by the density of the crop. In a thin braird of a grain crop more light reaches the lower internodes and branching (tillering) is encouraged. Conversely, in a thick-sown crop little light reaches the nodes near ground level and tillering is inhibited. A " thin " crop of a cereal tends to " thicken " up. Again, in flax when long straight unbranched stems are required for fibre the sowing rate should be heavy. If, however, the crop is being grown for the production of seed a thinner sowing gives more space per plant, therefore more light, and as a result more flowering branches per plant. The entire result in these two cases is not due to the light factor alone, for some of the response is due to heredity. In cereals, for example, there are free tillering varieties and others which tiller only sparingly (see p. 414) even when both are under equal conditions.

Light Quality and Growth

As regards quality or colour of light, it would appear that if the shorter wave-lengths are denied to the plant the internodes elongate unduly. When the blue end of the spectrum is admitted the internodes tend to be shorter. The more the light supply is restricted to long wave-lengths (red rays), the longer will the internodes be. The tissues, too, are very much altered in character by these variations in the quality of the light.

Photoperiodism

The reaction of the plant to different periods of illumination, that is, to different lengths of day or photoperiod, may be spectacular and depends on heritable factors. The ability to respond and the character of the response to any particular day-length is a racial or varietal character.

Some plants flower in response to a short day of about 12 hours, while a summer-flowering plant indigenous in the sub-polar regions is harmonized to a day-length of 15 to 20 hours. The onset of flowering is conditioned by day-length. Those plants which flower in response to a day-length of 10–14 hours are called " short-day plants," while those which require 14 hours or more are called " long-day plants." Plants which flower all year without regard to the length of day are termed " ever-blooming." The two classes of plant, long-day and short-day, may be either induced to flower out of season or remain in the

vegetative condition indefinitely by appropriate extension of the "day length" as by the use of artificial lighting, or shortening of the day as by shading.

In one kind of plant different varieties may respond quite differently. One variety may require short days, while another demands long days for flowering. From this we get "early" and "late" varieties. Control of flowering by manipulation of the photo-period is of use to those market growers who produce flowers or fruits out of season. It is also employed by the plant breeder who desires to make two plants of the same kind, but different behaviour to day-length, flower simultaneously so that they may be crossed.

Water Supply and Growth

The amount of the water supply affects growth rate. Unless the cells of the tissues are turgid, growth is not possible. As regards the root, water conditions are most important. As has been shown, the absorbing area of the individual root is not large, and is restricted to the short, uncuticularized portion behind the tip, usually supplied with root hairs. The movement of water through the soil to the absorbing region is not swift. Hence, if the water supply in the soil is restricted in amount, the root soon absorbs all the available water in its immediate vicinity. The soil in contact with the rootlet then becomes practically dry, though round about the apical portion, which absorbs but little, it is still somewhat moist. Growth of the tips in such a circumstance tends to be greater towards an area where new water supplies may be tapped. Roots therefore grow towards the more fully hydrated soil.

If, however, the root proceeds downwards and enters a level saturated with water, growth in that direction stops due to restricted air supply. In such a case active branching of the root occurs at levels just above the stagnant water. In a normal soil the roots rarely penetrate below the water-table, but are freely branched above it.

When the soil about a developed root becomes water-logged, as by a rise of the water-table through bad drainage or over-irrigation, those roots die. When the water falls away later and the water-table drops, the root system recovers, and will follow the falling water-level downwards. This is important in connection with crop production under irrigation. Irregular supply of water, too much at one time followed by too little at another,

may cause the lower part of the root system to die, and then later place a strain on the food reserves of the plant in redeveloping the system. The finest development of the root is in a soil well supplied with water, but where water-logging is prevented. Many varieties of rice (wet paddy) do best in water-logged soil, so too do osiers, but both of these are exceptional crops.

Vernalization

Temperature, light supply, and water supply all interact in the process of conditioning the plant through each of the stages of its life cycle from germination to flowering. It has long been known that some varieties of wheat have to be sown in late autumn if they are to come into ear for the subsequent harvest. Other varieties can be sown in the spring and yet ear well at harvest. "Winter" and "Spring" varieties of wheat are well known. If the water content of the seed of a winter wheat is raised and the grain then kept for some time at a temperature too low for germination, a physiological change takes place within it. Later it may be dried sufficiently to permit of easy sowing. Seed of winter wheat treated in this way and sown in the spring develops and ears satisfactorily. The seed shows no morphological reaction to the treatment, but obviously a significant physiological change had taken place.

Growth Differentiated from Development

From the results of experiments like these on wheat and carried out with many different kinds of plants, it has become possible to differentiate between growth and development; growth regarded as an increase in size; development as a sequence of internal physiological readjustments, which later find expression in morphological changes. In short, development is regarded as a series of physiological phases through which the plant must pass if the progression of morphological stages are to proceed normally. The physiological phases must be passed through, one after the other *and in their proper order*. Each phase requires for its initiation and completion an appropriate set of external conditions. The plant can be conditioned for each phase at almost any point of its life-cycle provided the proper order of phases is maintained. The embryo can be conditioned before growth commences!

Three separate phases have been recognized in winter wheat, with a possible fourth or transitional phase between the first two. The first two and the transitional phase are prerequisites for the production of floral organs, while the third or final phase is necessary for gametogenesis.

For the initiation and progress of the first phase temperature is the predominant member of the complex, while absence of light or subjection to a short day is secondary. In practice this happens when the seed lies cold and wet in the dark after sowing in autumn. The second and third phases are mainly conditioned by the light factor, and temperature is of little importance. With a normal autumnal sowing date a plant of winter wheat is usually subjected to just those conditions—cold with short days, followed by long days. It passes through the phases as it grows. The value of artificial conditioning is seen in a very cold climate, such as obtains in northern Russia, where winter killing of autumn-sown grain by intense frost commonly occurs. The seed of a winter variety may be treated under cover in a barn and sown in spring. The technique of passing a plant through its physiological phases artificially is called " vernalization," and the processes or reactions of the plant are referred to as phasic development.

Phasic Development in the Potato

The reaction of the potato to different photo periods will serve as a contrast to the behaviour of winter wheat, and show that different plants require different treatment. In potato flowering, fruiting, and tuber formation have each to be considered. Flowering, rhizome formation, and rhizome elongation are all favoured by long days, while tuber formation is favoured by short days. The details of the treatment appropriate to different varieties differs with the variety, for the character of the response made by a plant to length of day is inherited.

The " best " conditions for maximum crop yield in most varieties would seem to be, first, long days to stimulate rhizome formation, followed by a period under short days to induce tuber formation and swelling. The experimental data support the belief that " germinated " tubers can be put through the physiological phases conditioning stolon production and tuber formation prior to planting, and so permit the crop to use the whole growing season for the formation and enlargement of tubers.

Electric Currents and Growth

Other factors affect the growth of plants, for example electricity. Normally the air above and about the plant is electrically charged with respect to the earth, and the potential difference increases with height. Thus a plant growing up vertically has its top in an area of higher charge and its root in an area of lower charge. As a result the plant body will be traversed constantly by minute but measurable currents.

The natural potential difference may be artificially increased by placing a charged metallic screen over the plants. Current passes off the screen through the air and so to the plants. During experimental work carried out in England a current of 10^{-9} amperes was found to be definitely stimulating to growth. The power was supplied for part of the twenty-four hours only, and the stimulation appeared after the power to the screen had been switched off. Workers in the United States of America have not been able to obtain positive and confirmatory results despite a meticulous repetition of the experimental conditions used in Britain.

Growth in the Crop

In this chapter, so far, results obtained by measuring or observing the individual plant have been discussed. The farmer, however, is rarely concerned with single plants, it is the crop as a whole that constitutes his unit. A crop may usually be regarded as a group or population, and as soon as plants are grown together some degree of competition between plant and plant is introduced. The living space of each individual becomes limited. Most crops are grown in "pure stand"—that is, only one kind of plant barring weeds is in the field at one time. Typical examples may be seen in a really clean crop of potatoes or of oats. Other crops, such as oats with beans, or pasture, are mixtures of different kinds of plant.

The pure stand is simpler in character than a mixed crop. Here each individual competes only with a plant of similar structure and capability. The intensity of competition to which any one plant is subjected under these conditions depends only on the spacing or distance between each and any special arrangement of the plants.

An isolated plant of any kind given unrestricted "elbow-room" takes a characteristic shape. The root runs through a region of the soil in shape somewhat like an inverted cone. When-

ever a number of plants are growing near together their root systems tend to encroach on each other. The encroachment or overlap between root systems does not go far, for branchlets of one will not exploit a region the other plant has already dried out. The volume of soil occupied by each plant's roots under condition of close planting soon ceases to be cone-shaped and becomes roughly cylindrical.

Competition between adjacent shoot systems, too, results in restriction of the space occupied by each. Overlapping of shoot systems causes reduced light supply followed by restricted branching. Restriction of branching may be reflected on yield directly, for the number of leaves, flowers, and fruits depends on the production of sufficient branches to bear them. If any of these parts be the object for which the plant is grown, a direct drop in yield follows.

Further, restriction of leaf soon restricts the total amount of photosynthesis and the rate of dry matter accumulation falls.

These basal facts apply to the behaviour of the individual plant in the crop. The figures of importance in practice, however, are not those of yield per plant, but yield per unit of area occupied by the crop. As the number of plants in unit area (population density) rises the yield of each plant falls, but the yield *per unit of area* will not fall in the same way. This point is well brought out by work done on the cotton plant in Egypt.

Competition and Yield in a Cotton Crop

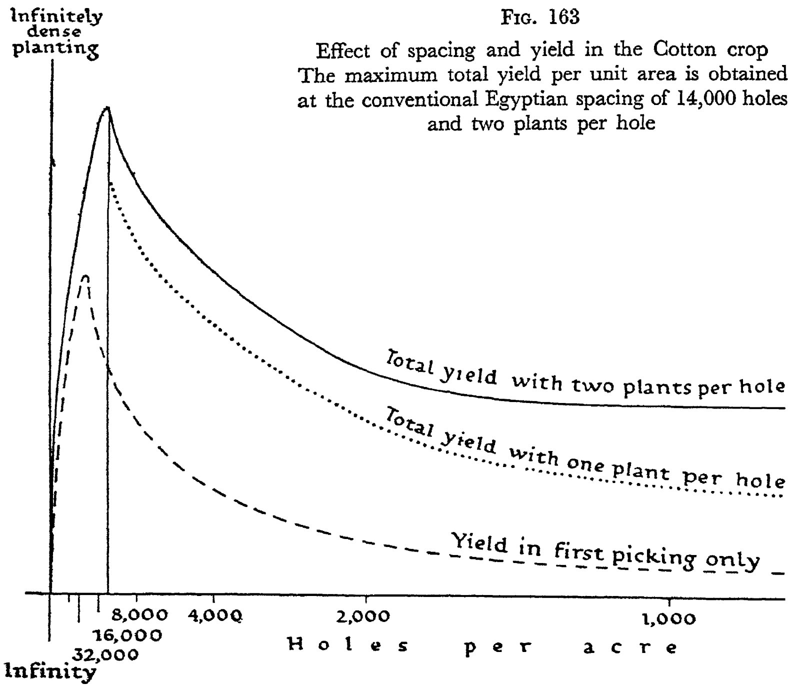
This crop is grown in rows, the seeds being dropped two at a time into holes in line. Two seedlings appear from each hole. One seedling of the pair may be thinned out, or both may be allowed to develop. If both are allowed to remain and grow, inter-plant competition for living space is intense and the yield per plant drops very steeply, but not to half of that produced by one plant per hole. The two plants per hole together produce 10 per cent. more than does one plant per hole. Yield per acre in this case is 10 per cent. higher than where only one of the plants is allowed to survive. The facts are well illustrated by Fig. 163 overleaf.

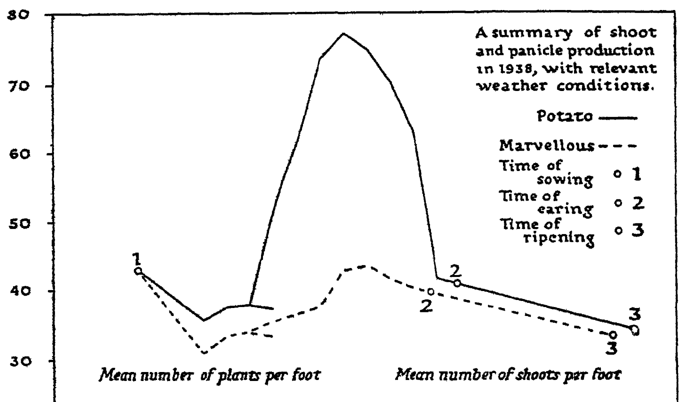
Competition and Yield in a Cereal Crop

Shoot and root competition interact in producing still further effects. In the oat plant, for example, light causes increased tillering, but root competition may so restrict feeding room that the

Fig. 163

Effect of spacing and yield in the Cotton crop
The maximum total yield per unit area is obtained at the conventional Egyptian spacing of 14,000 holes and two plants per hole





	MARCH	APRIL	MAY	JUNE	JULY	AUGUST
Mean air temperature (°F)	47·7	46·1	49 0	54·8	57·5	57·2
Difference from average	+ 7·4	+ 2·4	+ 0 1	+ 0 6	− 0·2	+ 0·1
Rainfall (inches)	0·57	0·15	4 18	2·87	2·43	1 15
Percentage of average	29	10	204	143	86	(not available)

Fig. 164

The tiller and panicle production of an Oat crop in Scotland
(*From S. G. Stephens, Thesis, Edinburgh University*)

tillers produced cannot do much good. This is well brought out by Fig. 164. This shows the history of an oat crop grown in East Scotland. The sowing rate of 4–5 bushels per acre is normal for the district. At this sowing rate the crops tiller freely, but these branches are of no value, for the number of heads (panicles) harvested is exactly as the number of individual plants. Tillers are produced freely, but they do not come to fruition. In short, tillering, though it " thickens up " the crop and prevents weeds, adds only to the straw but adds nothing to the yield of grain per acre.

Competition between Plants of Different Habit

When a mixed association comes to be considered, competition between the different kinds of plants varies with the nature of the plants involved. Two kinds of plants of dissimilar habit may " fit in " so as to fill the space available to them with the minimum of competition. This is seen when a plant of tufted habit is grown in association with a surface creeper. An outstanding example of such a happy intermingling is seen in an association of perennial ryegrass and white clover. Other " pairs " may not fit in at all well and are antagonistic. For example, a fast-growing tall grass with broad leaves carried well up the stem will shade and overcome a dwarf growing grass no matter how vigorous the latter may be. These aspects of inter-plant relationship will be discussed more fully in connection with pasture formation on the one hand and weed elimination on the other hand. Suffice it to say at this stage that plants do compete, both at their roots in the soil and at their shoots in the air, as soon as the density of planting brings the margins of their living space together.

BOOKS FOR FURTHER READING

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PEARSE, H. L. *Plant Hormones and their Practical Importance in Horticulture* (Imperial Bureau Horticultural Plants, Technical Communication No. 12, 1939)

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THOMSON, B. F. " Tissue Responses to Physiologically Active Substances " (*Botanical Review*, 11 (10), 1945)

CHAPTER XX

THE SEED

GERMINATION

A MOST critical phase in the growth and development of the plant comes when the seed which has lain quiescent for a time embarks on the train of events which leads to the production of a functioning plant—germination.

As seen in the study of anatomy the unit which is called a seed in practice may be any one of a whole series of different structures. It may be a true seed, that is, a whole ovule after fertilization and maturation have been completed. Or it may be a fruit which is a ripened matured gynæceum or part of one. Extra structures may be included as in mangold where a persistent calyx, torus, and even a bract may form part of the "seed." In many grasses the "seed" is a fruit enclosed in two or more enveloping leaves of the nature of bracts or bracteoles. The "seed," no matter what its botanical nature (apart from structures of a purely vegetative character), is essentially an embryo plant associated with stores of food and all enclosed within coverings.

This biological unit, with all its vital functions reduced to a very low ebb, when subjected to appropriate conditions becomes reactivated, and the process of germination ensues.

Given a living (viable) seed, the conditions necessary for germination are, a suitable supply of moisture, an appropriate degree of heat, and sufficient oxygen. When these conditions are present, and the seed has no special idiosyncrasies, the unit commences to rehydrate and water is imbibed. Hydration is followed by a reactivation of enzymes and food reserves commence to hydrolyse. As the stores of food take simpler forms respiration develops, and is soon followed by active cell-division in the embryo itself. The train of events, then, is hydration $\longrightarrow$ hydrolysis $\longrightarrow$ respiration $\longrightarrow$ growth. One step does not await the completion of the previous one before action starts, nor does it cease on the commencement of the next, but the steps commence in the order shown and are interdependent.

Intake of Water by a Seed

Typically, the intake of water depends on two distinct mechanisms. One is the hydration of the colloidal material of the tissues, and almost invariably the outer coverings attain a high water content before the inner tissues take in any very significant quantity.

In seeds the rehydrated outer covering in almost all cases behaves as a semi-permeable membrane and water enters the space between the coverings and the embryo by osmosis. In seeds like the broad bean this sets up a quite distinct pressure. The semi-permeability of the coat may be demonstrated by an osmometer as shown in Fig. 165.

The seed increases in total weight as the water passes in. If periodical weighings of an individual seed are made while it hydrates, this increase often shows two phases. Firstly, the phase of colloid hydration, and a subsequent phase of osmotic intake. The increases in weight when plotted against time show two "peaks" as shown in Fig. 166. The micropile is seen as a relic in many true seeds, and some investigators believe that water passes down this channel into the embryo.

Of the inner parts the embryo is usually the first to rehydrate. In endospermic seeds the part of the endosperm next to the absorbing organ of the embryo shows liquefaction at about the same time. Hydrolysis of foodstuffs and hydration of the embryonical axis go pretty well hand-in-hand. Respiration comes in too at about the same time. Very soon the

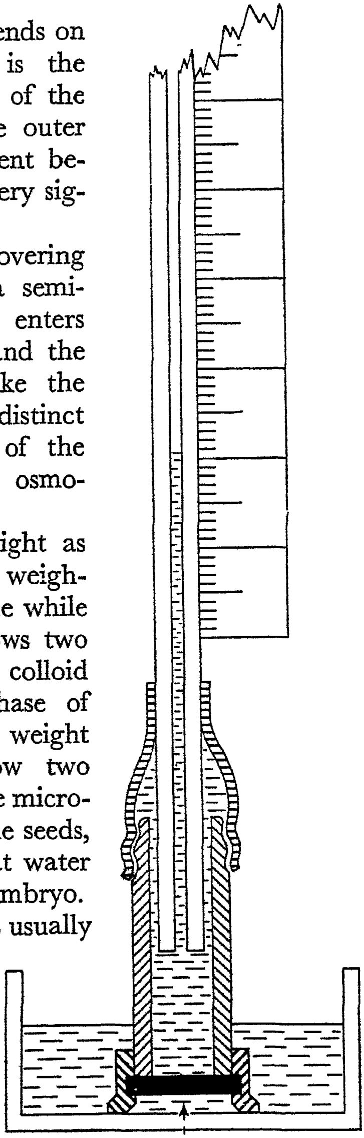


FIG. 165
Osmometer with testa acting as a semi-permeable membrane

primary meristems of the plumule and radicle show active cell-division, and the process of germination is completed. In practice, a seed is held to have germinated only where the seedling appears above the surface of the soil. This is a very late stage and depends on growth after germination. The Scots word braird suits better as a term describing the appearance of the seedling above the ground.

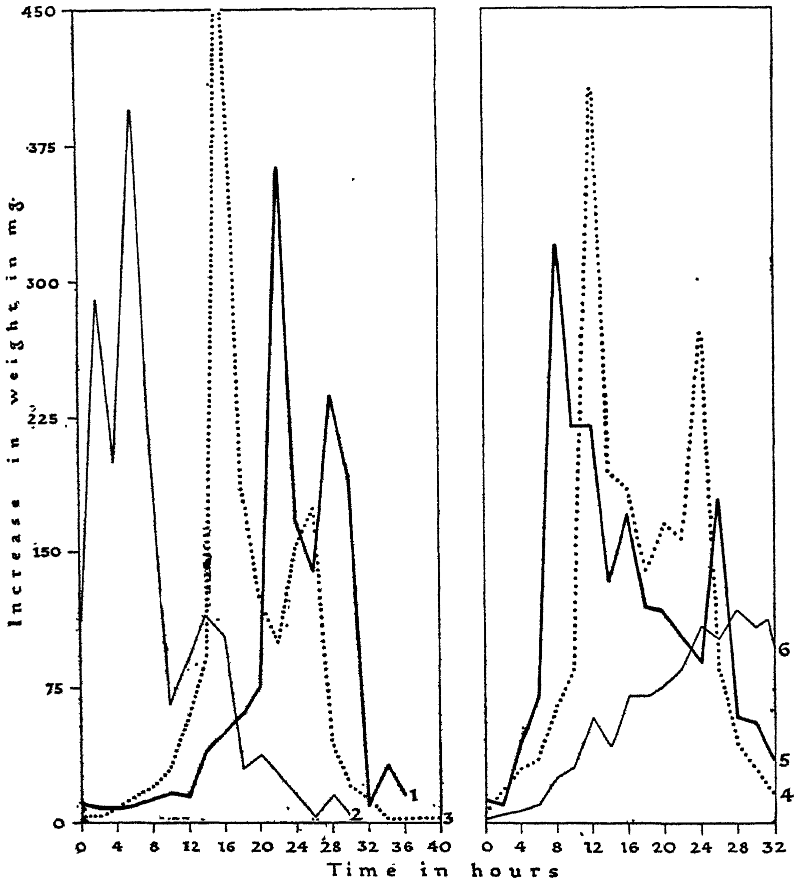


FIG. 166

Water intake by Seeds

Curves showing the rate of water intake by six broad bean seeds. Each shows individual characteristics but all show two main peaks: the first peak is believed to be associated with colloid hydration, the second with osmotic intake

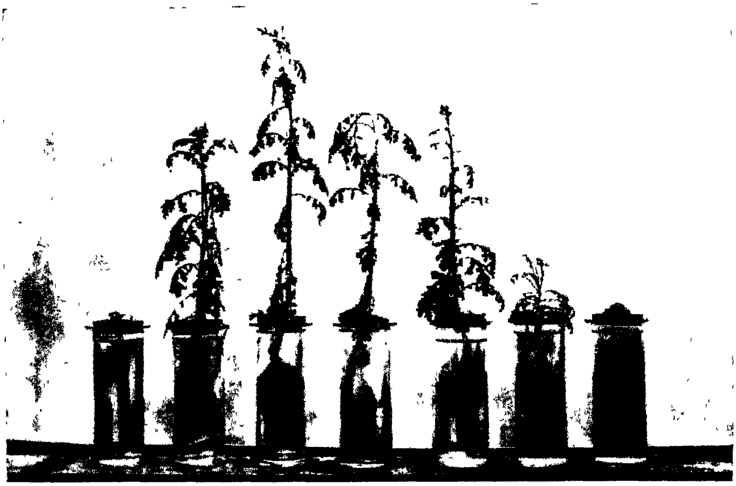
PLATE 71 RICE AND PASTURE

Rice crop in Malaya. This grass requires plenty of water

Pasture Analysis. Note the use of a quadrat

pH 2 2·5 3 4 5 6 6·5 7

WAVY HAIR GRASS (*Deschampsia flexuosa*)



pH 3 3·5 4 5 6 6·5 7

RAGWORT (*Senecio sylvaticus*)

pH 3·5 4 4·5 5 6 7 7·5

COLTSFOOT (*Tusilago farfara*)

These different plants do best at different H.I.C.

(*From Carsten Olsen C. R. Lab. Carlsberg. 15 (1), 1923*)

Failures in Germination

The actual mechanisms involved in true germination are of considerable botanical interest, but in agriculture importance attaches more to those cases where the train of events fails and the embryo though not dead does not become functional.

External Causes

The causes of these failures may be considered in two classes. First, there are those cases where some external factor is not satisfactory ; and secondly, cases where some idiosyncrasy of the seed mitigates against success.

Water Supply

In the first class is water supply. If water supply to the seed is too low, rehydration cannot proceed to a sufficient degree. On the other hand, if the seed is completely bathed in water, germination may not proceed because the liquid does not supply sufficient oxygen to meet the relatively enormous demands of seed respiration. Further, carbon dioxide tends to accumulate in the water.

This is one of the reasons why steeping seed in water or in watery solutions before sowing must be carried out with care. Some kinds, *e.g.* carrot and parsley, tolerate and indeed benefit from pre-soaking for quite long periods of, say, twenty-four hours or more. On the other hand, runner bean will not germinate successfully if steeped for more than one or two hours before sowing. Some seeds, like those of mangold and beet, if pre-soaked exude a substance into the water, and this seems to poison the embryo. A mass of soaking beet seeds can poison themselves in quite a short time unless the water is frequently changed.

Solutions of chemicals must be used with care in pre-soaking seeds. Water intake may be reduced or retarded if a soluble substance is present in sufficient quantity to counter the physical forces causing rehydration. This sometimes happens in the field when seeds are sown in the soil along with a highly soluble manure.

Often, in order to combat disease, seed is sterilized on the surface before sowing either by immersing it in a poisonous liquid or covering it with a poisonous dust. If this poisonous seed-dressing gains admittance into the body of the seed the embryo may be killed or seriously damaged. Some degree of protection

against this danger is obtained by using as the dressing a substance with a molecule which cannot pass through the seed coverings.

If too much of the dressing is used, and a comparatively large quantity of the poison remains adhering to the seed when it is sown, there is danger that when the young root emerges damage to it will result.

Temperature

As regards temperature, seeds vary in their demands but few if any germinate well at low temperatures. For most crop plants a temperature about 20° C. seems to be best. Below this, germination is slow, above it the seed may " go to sleep." That is to say, it rehydrates but proceeds no further. For many seeds such as clover the best condition is a constant non-fluctuating temperature, but for others this results in a very low or nil germination. For example, seeds of the meadow grasses demand for quick and full germination a fluctuating temperature : that is, 30° C. during the day (8 hours) and 20° C. during the night (16 hours).

Light

Many seeds are sensitive to light. Some germinate best in the dark, while others require to be illuminated for at least some part of each twenty-four hours. The relationship between light, temperature, and germination is brought out in Fig. 167.

There is a widely held belief that seed germination may be affected by moonlight, and that times of sowing should be decided by reference to the phases of the moon. Evidence in this regard is conflicting, but what is available points to the belief being fallacious.

The idea may have arisen from the fact that selection of a suitable sowing date is of considerable importance in obtaining a satisfactory braird. If weather conditions and phases of the moon are related, then some aspects of the moon may be more suitable because accompanied or followed by more propitious weather.

Conditions in the Soil

If put in the soil too early, seeds run great risk of becoming waterlogged and rotting off, because of temperatures being too low and rainfall too copious. Even if the early sown seeds do germinate the process will be slow.

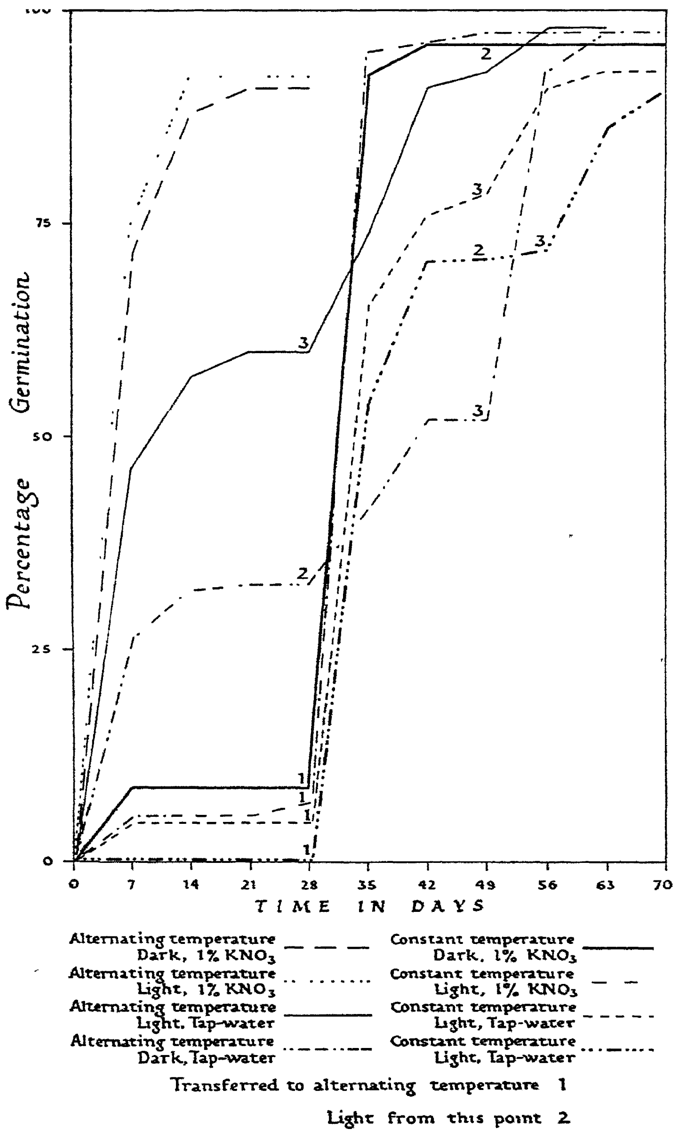


FIG. 167

External conditions affect germination
(Data for Canada Blue Grass)

This delay provides the enemies of the seeds (birds and soil organisms) with a longer period for their depredations, and the consequent loss of seed shows in a thin braird.

Too late a sowing, on the other hand, while likely to be under more favourable temperature conditions, may easily encounter low water supply, at least where the seed is situated in the upper layers of the soil. Dry conditions of this surface layer may arrest rehydration of the seed, or more serious still, may dehydrate the developing seedling before it is rooted in the soil.

A decision as to the optimum depth to which seeds should be sown in the soil (apart from questions of light sensitivity) is conditioned by attempting to compromise between the capacity of the food reserve they contain and the beneficial effect of deeper rooting.

Seeds with a large food reserve can be planted deep. They have the material to provide for sufficient growth to enable the young shoot to reach the surface and commence synthesis. An apparently large " seed " however, may not contain copious food reserves. For example, the so-called seed of mangold or beet appears to be large, but as it is an aggregation of two or three quite small seeds, each with no great food reserve, it should not be buried deep.

The seed-bed should be as fine as possible, for if there are large clods and the surface is rough or stony many seeds may be covered in such a way as to prevent the young shoot reaching the light.

Characteristics of the Seed and Germination

The characteristics of the seed which affect the success or failure of germination form two sub-classes. On the one hand there are those features which pertain to the outer coverings, and on the other hand those which belong to the embryo and its attendant structures.

Seed Coverings

The seeds of linseed, plantain, white mustard, and many others, when wetted, exude mucilage. This mucilage has a use very similar to that of the hairs on the outer epidermis of the cotton seed. The covering of hairs or mucilage is an extremely powerful binder of water. When wetted it attracts and holds moisture. If the water present is less than sufficient for the full

saturation of the external covering, it holds water tenaciously and prevents the embryo from receiving a supply. This delays germination.

Surface hairs and mucilage, though they may delay germination, are useful in dry climates. When the first rains at the beginning of the growing season fail and drought conditions recur temporarily, the mucilage, once wetted, maintains round the seed sufficient moisture to prevent the drought reaching the partially reactivated embryo, and so carry it over till the true rains fall. In commercial cotton-growing the seed hairs are removed before sowing, and then under good water conditions germination is prompt and regular.

Clovers and other legumes often produce seeds which, when wetted, fail to absorb water, and so do not swell up and germinate, but remain indefinitely hard and inactive. These are called " hard seeds." This impermeability to water seems to be located at or about the surface of the testa, for if a " hard seed " is scratched water is taken in freely and germination is prompt. In the soil frost, alternations of temperature, the abrasion of shifting sand, the activity of soil organisms, all serve to rupture or scratch the coat, and in time the hard seed germinates.

Seeds are known where the coverings are impermeable to gas (oxygen passing in or carbon dioxide diffusing out), with the result that germination is prevented.

The Embryo

Let us now turn to consider those characteristics of the embryo which cause delay in germination.

It has long been known that after harvest physiological processes continue in the apparently inert seed, and until these changes have been completed the seed will not germinate. Fresh, newly harvested seed often fails to germinate even though given perfect conditions. This seed is said to be " harvest ripe," but not " germination ripe." Seed in this condition requires time to complete its physiological development. Some non-germinating ripe seeds, such as turnip, will " ripen " during a comparatively short period in normal storage, but others demand special treatment.

Many non-germination-ripe seeds must be specially stored if later they are to respond to suitable germination conditions. Pretreatment in these cases is done by placing the seeds in damp

peat moss or sawdust, maintained at a temperature at or just above freezing point. This treatment is often referred to as *stratification.*

Seeds of plants from areas of hot, arid summers seem to require treatment the converse of stratification. These demand storage under relatively hot dry conditions. These facts show that many seeds are harmonized to the climate of their natural habitat, and that they will not germinate unless stored for at least part of the period between harvest and sowing under conditions which simulate what would be their normal experience under natural conditions.

Storage of Seeds

Storage conditions for seeds in general must be carefully controlled. Most seeds if stored damp at normal temperatures will increase their usual minimal metabolic activity and "burn themselves out." Damp storage, especially if accompanied by higher temperatures, will certainly weaken the seed, if not kill it, in a very short time. Dry storage at as low a temperature as possible in sealed containers suits most crop seeds and preserves their viability. Seeds of *Spartina Townsendii* (a grass) and sugar maple (a tree) are outstanding exceptions to this otherwise quite general rule. If dried out these seeds rapidly lose vitality. Seeds of water plants also tend to show this characteristic.

Establishment of Seedlings in the Soil

Given that storage and germination have been successfully passed, the next stage in the life of the plant in the soil is establishment. This is difficult to define. Briefly, establishment relates to the fixing of the young root in the soil, and the adjustment which must take place between its shoot and that of its neighbours.

In pasture plants, establishment value has been defined as "the number of individuals which, in the soil, reach the spring following the seeding year, expressed as a percentage of the number of viable seeds sown." Successful establishment in this definition includes germination. The figures for establishment are spectacular in their smallness, and indicate why seeding rates have always been very much higher in practice than the theoretical requirements.

The considerable loss of seed in the soil is brought out clearly

by the table on pages 390–391. Even in the case of ryegrass, one of the most successful pasture plants in this regard, one-third of all the viable seed sown fails to establish plants. With the small-seeded grasses some 90 per cent. or more of the living seed sown fails to produce a plant in the soil. These figures apply to tests made in a garden ; the results from field conditions would probably provide the same relative order for the different kinds, but the figures would be reduced.

Sowing dates	Perennial rye-grass	Tall oat grass	Cocks-foot	Timothy	Crested dogs-tail	Suffolk red clover	Alsike clover	Wild white clover
Average of 6 sowing dates, Mar. 1–May 10 . .	78·7	56 5	48·8	37·9	27·4	64·7	60·5	55·1
Average of 6 sowing dates, May 24–Aug. 2 . .	65·0	57·3	48·4	48·1	29·7	59·0	34·5	42·1
Average of 3 sowing dates, Aug. 16–Sept. 13 . .	80·9	59·1	49·4	45·8	36·6	16·3	14·9	13·0
Average of 3 sowing dates, Sept. 27–Oct. 26 . .	69 9	42·0	18·9	31·7	10·3	1·9	0·5	2·7

Table showing the average percentage establishment for eight typical species from eighteen sowing dates in 1923 in *Garden Trials*, 1923

(*Extracted from Stapledon & Co-workers' Bulletin H6, Welsh Plant-Breeding Station, 1927*)

Time of Sowing

The time of sowing affects the figures for establishment. Some sowing dates are more favourable than others. This is brought out in the table above.

The weather after sowing, the nature of the soil, and the water supply are doubtless the major factors influencing success or failure.

It is to be seen in the table that the optimum sowing period in Wales is in the month of April. Sowings made prior to that date give low figures for establishment. The adverse effect of early sowing is probably due to the low temperatures obtaining at that time, and perhaps too much rain. With the advance of the year the tendency is for the figures to fall after April. The figures for mid-June, which in this experiment coincided with a spell of very dry weather, were low. One point of great importance brought out by this table is the depressant effect of late sowing on the establishment of clovers.

Line	Species and strains.[1]	Lab. germination	Results for 1923: Percent. establishment of viable seed: Average of 18 sowings Mar. 1–Oct. 26	Average of 6 sowings Mar. 1–May 10
1	Italian Ryegrass	88	70·4	79·5
2	Perennial Ryegrass commercial	94	73·0	78·7
3	Perennial Ryegrass indigenous	—	—	—
4	Cocksfoot commercial	94	43·7	48·4
5	Cocksfoot indigenous	—	—	—
6	Tall Oat Grass	93	54·8	56·5
7	Timothy	98	41·5	43·0[2]
8	Meadow Fescue	96	23·9	30·5
9	Tall Fescue commercial	—	—	—
10	Tall Fescue indigenous	—	—	—
11	Chewing's Fescue	85	46·5	53·8
12	Meadow Foxtail	73	27·5	31·8
13	Crested Dogstail	96	26·8	27·4
14	Rough Stalked Meadow-grass	92	9·2	9·2
15	Smooth Stalked Meadow-grass	—	—	—
	Average of all grasses	90·9	41·7	45·8
16	Lucerne	—	—	—
17	Montgomery Red Clover	96	27·5	43·7
18	Suffolk Red Clover	89	44·2	64·7
19	Chilian Red Clover	—	—	—
20	Alsike Clover	90	34·2	60·5
21	Wild White Clover	78	35·0	55·1
22	Subterranean Clover	—	—	—
	Average of all Clovers	88·2	35·2	56·0

[1] When no qualification the seed was ordinary commercial
[2] Period March 1st–August 2nd

(*From Stapledon and Co-workers' Bulletin H 6.,*

Line	Results for 1924			Results for 1925		
	Lab. germination	Percent. establishment of viable seed		Lab. germination	Percent. establishment of viable seed. 2 sowings Mar. 16–Apr. 17	Average percent. establishment for two or three years [2]
		Average of 18 sowings Mar. 6–Oct. 31	Average of 7 sowings Mar. 6–May 27			
1	—	—	—	84	52·1	65·8
2	93	70·2	74·1	89	44·4	65·7
3	94	78·2	79·0	—	—	—
4	92	29·5	36·2	93	39·5	41·0
5	88	37·7	40·2	73	20·4	30·3
6	—	—	—	90	48·4	52·4
7	—	—	—	97	37·7	40·3
8	—	—	—	93	62·1	46·3
9	—	—	—	90	48·4	—
10	—	—	—	82	39·8	—
11	—	—	—	67	32·4	43·1
12	—	—	—	60	9·6	20·7
13	—	—	—	88	12·0	19·7
14	—	—	—	90	5·2	7·2
15	—	—	—	82	2·2	—
	91·7	53·9	57·4	84·1	31·4	39·3
16	—	—	—	85 + 1 [4]	47·4 [5]	—
17	—	—	—	72 + 4 [4]	41·1	42·4
18	—	—	—	—	—	58·2
19	—	—	—	95	51·8	
20	—	—	—	98 + 1 [4]	55·1	57·8
21	—	—	—	90 + 2 [4]	46·6	50·8
22	—	—	—	36 + 29 [4]	35·0	—
	—	—	—	79·3 + 6·1	46·1	52·3

[2] The sowing dates March–May are here averaged
[4] Hard seed
[5] Establishment from the five most successful sowing dates, March 30th–August 4th

Welsh Plant-Breeding Station)

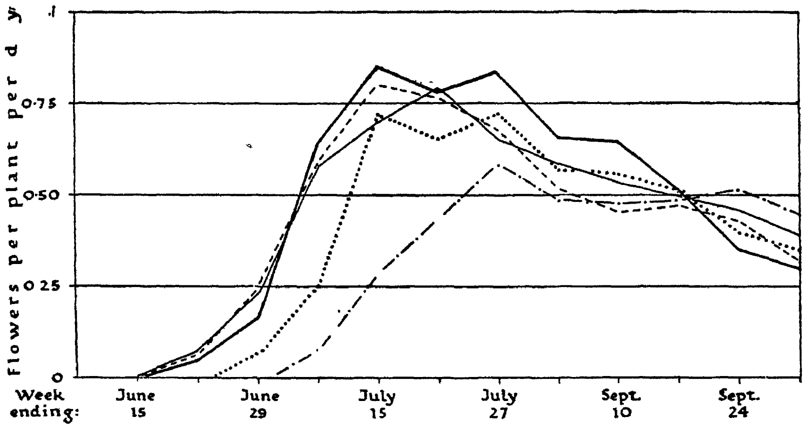


Fig. 168

The effect of sowing date on flowering in the cotton crop

- - - - - - - - - sown one month before usual date
———— sown a fortnight before usual date
———— sown on usual date (15th March)
.... sown a fortnight after usual date
—·—·— sown a month after usual date

(*From W. L. Balls,* "*Developments and Properties of Raw Cotton*")

Concentrating only on botanical considerations and ignoring any question of practical convenience, it might be thought that earlier sowings would be preferable to late sowings. This, by giving the plant an earlier start and possibly a longer growing season, might be expected to provide a heavier crop or an earlier harvest. If this were so the cultivator might be tempted to take advantage of suitable weather in spring to push on the work and sow early.

The low figures for establishment resulting from early sowing would argue against rushing the seed into the soil. This disability could be got over by increasing the amount of seed sown per unit of area, but it is questionable if this is worth while, on the point that yields are not greatly increased by sowing earlier than is normal. It may be said that for each crop in each district there is an optimum date for seeding the land, and that any deviation from it to an earlier or later date is not to be recommended. Local tradition and practice in each district over the years has defined this date, and it may not be ignored with impunity.

Sowing date	Pickings (bolls per plant)			Total bolls per plant	Five bolls ripe—date
	First	Second	Third		
Feb. 15 . .	6·17	4·87	3·72	14·75	Sept. 2
„ 22 . .	7·32	5·97	3·14	16·43	Aug. 30
March 1 . .	6·82	4·53	3·39	14·72	„ 31
„ 8 . .	7·36	4·89	3·11	15·35	„ 30
„ 15 . .	6·85	5·93	3·21	16·00	„ 31
„ 22 . .	5·70	5·46	3·69	14·88	Sept. 3
„ 29 . .	4·85	5·00	3·38	13·20	„ 9
April 5 . .	3·07	5·18	4·12	12·39	„ 13
„ 12 . .	2·38	4·39	4·05	10·80	„ 18

Conventional pickings and final yield in cotton

The pickings are expressed as the number of bolls per plant. The approximate dates on which five bolls per plant had been ripened are also given

(*From W. L. Balls and F. S. Holton, Trans. Roy. Soc.* (*London*), *B. 206, 1915*)

Relationship between Sowing Date and Yield

This relationship is very well shown by experiments with the cotton plant in Egypt. The harvest in the case of this crop is the ripe seeds, and hence figures for the yield express a summation of the whole history of the life cycle of the plant. The date of sowing traditionally observed by the native cultivator near Giza, where the experiments were carried out, is on or about March 10th. If conditions at that time do not permit him a free choice the native seems to prefer to sow after, rather than before, the usual day.

In the experiments, the yields obtained following nine sowings made at weekly intervals from February 15th to April 12th showed the optimum date to be March 15th—five days after the native cultivators' chosen date. It was also shown that the choice of the slightly earlier than optimal sowing, while it made little appreciable difference to final yield, did permit of partial resowing if the first sowing failed. In short, local custom had found the earliest date likely to give a successful crop, and still permit of a resowing at a sufficiently early date if such were required (see table on page 394).

That earlier sowing did not advance the date of harvest is shown by Fig. 168, which summarizes all flowering dates of the plants sown at different times. That early sowing does not materially advance the date of harvest, and in

Time of Sowing	No. of Plants	Number of bolls ripened in week ending											
		August					September				October		
		2	9	16	23	30	6	13	20	27	4	11	18
February 15	594	15	106	382	947	1,141	1,085	1,065	954	879	823	756	635
February 22	645	18	93	430	1,186	1,489	1,513	1,454	1,216	1,188	798	713	512
March 1	717	10	90	490	1,146	1,619	1,537	1,312	1,038	902	929	866	639
March 8	717	10	94	546	1,283	1,786	1,556	1,605	1,157	743	816	823	586
March 15	776	5	67	335	1,389	1,865	1,660	1,837	1,401	1,359	1,087	766	636
March 22	750	2	48	390	989	1,540	1,313	1,585	1,332	1,181	901	1,189	675
March 29	729	—	6	151	726	1,458	1,302	1,471	1,163	1,109	1,000	804	733
April 5	694	—	—	26	342	752	1,015	1,309	1,196	1,093	1,042	820	998
April 12	739	—	—	11	179	621	948	1.239	1,012	996	1,040	1,045	909

Relationship between sowing date and yield

(*Extracted from Table XII, W. L. Balls and F. G. Holton, Analyses of Agricultural Yield Trans. Roy. Soc. (London), Series B, Vol. 206, 1915*)

addition does not lead to an increased yield, is shown in the table opposite.

The date on which the first five fruits (bolls) were ripe and fit to pick is shown, as well as the yields from the pickings expressed in terms of bolls per plant. The delay in the onset of harvest and the delay in the onset of main yield is well brought out.

It has been implied in discussing sowing dates that the history of the development of a plant through its normal growing period fits a conventional pattern. Each stage in development occurs in proper order, and there is a constant relationship in time between each stage. That this is so is of considerable use in practice, for quite early in the history of the crop it is possible to forecast its behaviour in the future. For example, in cotton where detailed information as to the course of development is available, it is possible at quite an early stage to say at what time the harvest will occur and how long it will take to complete. Fig. 169 brings out this point.

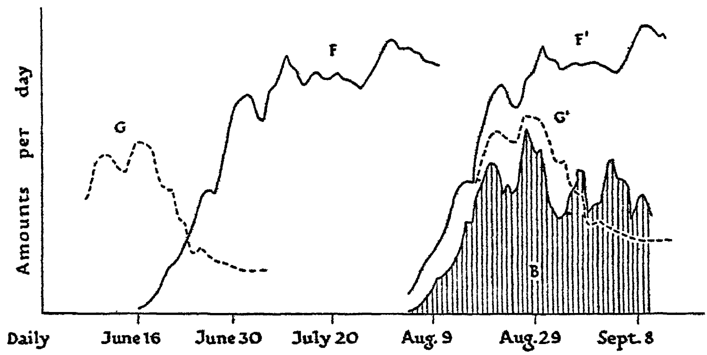


Fig. 169

Plant development curves and their use in forecasting

G = Daily growth of the main stem F = Flowering curve (number of flowers opening each day) B = Number of Bolls (fruits) ripening each day (harvest) G[1] is G moved forward 74 days F[1] is F moved forward 51 days. Note that G and F closely resembles the early part of B and thus the date of harvest can be foretold 2½ months in advance

(*From W. L. Balls, Development and Properties of Raw Cotton*)

BOOKS FOR FURTHER READING

Crocker, W. "Life Span of Seeds" (*The Botanical Review*, 4 (5), 1938)

Balls, W. Lawrence. *The Cotton Plant in Egypt* (Macmillan, London, 1919)

Balls, W. Lawrence. *Development and Properties of Raw Cotton* (A. & C. Black, London, 1915)

Chapter XXI

PASTURE

It has been shown that plants are considerably affected by the soil they grow in, the climate about them, and the competition of their neighbours. In addition, the animals which feed on the plants exert a powerful influence on their behaviour. The study of the action of all these factors and their effect on the success or failure of the plants in an area is the science of plant ecology, or the study of the plant in relation to its environment. It is to the wild plant in its natural surroundings that this part of biology is usually directed.

In agriculture, pastures approach more or less to this condition. Pastures on the poorer lands, those on which it does not pay to apply manure or otherwise expend capital or labour, are in a state of nature except for man's partial control of the stock. The whole range of pasture work extends from those sub-marginal areas through all gradations to the highly manured, carefully managed pasture on fertile land. The problems of them all are problems of the plant in relation to its environment; the most significant difference between them is the degree of man's control.

A pasture may be defined as a crop of mixed herbs receiving little or no cultivation after initiation and fed to stock *in situ.* The mixture, or association as it is termed, may be simple, of only one or two kinds of plant, or it may be complex and contain many different species. Typically, it is composed of grasses and clovers, but many miscellaneous plants may also be included, as, for example, chicory, medick, yarrow, and so on. The degree of cultivation may be nil or never rise much above surface harrowing of greater or lesser severity. Generally, pasture is "harvested" by grazing, but the produce may be cut and dried and utilized as dried grass or as hay. The same sward may be grazed at one time and provide forage or hay at another time.

The pastures may be started by nature and "just happen" to give the truly *natural* pasture. Those in Great Britain occur only on the poorest land, but much of the great grazing areas overseas is natural pasture. Arable land gone out of cultivation for economic or other reasons is sometimes allowed to

" tumble down " to a natural mixture of the plants whose seeds were already in the soil or are carried into the area by natural agents. In a sense these are natural pastures. In countries where the system of agriculture is intensive, when natural pasture is referred to it is often old grassland that is meant. The converse of the natural is the artificial or sown pasture.

In practice " natural " is synonymous with " permanent " pasture, and means, " in existence, or intended to exist for a long time." The converse of the permanent pasture is the temporary ley, a pasture down for a short time, and often, because it takes a place in a rotation of crops, called rotation grassland.

There are other useful systems by which pastures may be classified, but the only one of importance at the moment is that based on the botanical composition of the sward. The predominant species in the herbage is used to designate the whole; *e.g.* " ryegrass," or " ryegrass/white clover."

Pasture Analysis

The methods by which pasture is analysed into its components and their production ascertained vary. Under an extensive system of agriculture mere general inspection will often suffice in simple cases. When the composition of the sward is required with some degree of detail, special methods of botanical analysis must be used. No one method will satisfy the various requirements of different inquiries. There is considerable difference between the kind of information required from the survey of a large virgin colonial area for purposes of settlement, at one extreme, and the investigation of a highly developed meadow at the other. In the first of these examples, a somewhat cursory examination of the area will often provide data permitting the boundaries of each of the various associations to be mapped. If areas are occupied by species occurring practically pure, these may be marked in on a map. In either case sufficient notes should be made regarding apparent productivity.

In slightly finer work, in rather smaller areas, the number of times or frequency with which the various species occur in the different associations can be noted. These are simple cases. In artificial grassland under more intensive conditions pasture analysis in its formal sense has to be more detailed and concerned with quantitative rather than with qualitative data. Two

main systems exist. On the one hand there is the evaluation of the proportions of the total area covered by each species. On the other hand there is the assessment of the weight of herbage produced by each species within the area. The weight method may be further refined by estimating separately how much stem, leaf, and flower there is of each species. The two approaches, area covered and weight produced, may be compared with two surveys of a forest. An observer in an aeroplane could enumerate the species appearing in the topmost layer of the wood, and so give the frequency with which each occurred. In the other a forester on the ground could enumerate all the kinds of plants in the forest from the ground up, and assess the total bulk of each.

Both surveys would have a value, for in the first the tallest trees, and therefore those contributing most to the total bulk, would appear in their proper proportions. In the second, the figures might be more precise and detailed, for they would include low-growing and perhaps valuable types. Which method to adopt in pasture work depends on the purpose for which the data are required.

Sampling the Pasture

It is not practicable to analyse a whole field in detail by either method, and therefore sample areas must be used. These sample areas should be chosen at random. Once the areas have been marked off a turf of known dimensions may be cut out and taken to the laboratory and the various components enumerated there. A patch of the grassland may be marked off with a frame of wood or wire, or an area traced out by a line on a peg and these analysed *in situ*. The sample areas, no matter how delimited, are known as quadrats, and each is usually one metre square.

Another method of sampling is seen when a straight line of known length is laid out across the pasture and the required details noted all along it. In order to reduce labour, only those species may be recognized which occur at points regularly spaced along the line. The line or line of points may be called a line quadrat, or a series of point quadrats. If the complete line is used in analysis it may be called a transect.

The Data obtained from Pasture Analyses

The data to be accumulated, whatever method of analysis is adopted, depend on the nature of the inquiry. The number of

times each species occurs in a hundred individual readings provides the " specific frequency " of each. In this case many appearances of a small dwarf plant in a mixture will rank high, while the occurrence of a few plants of a large-growing, productive species associated with it will rank low. From the point of view of a farmer with beasts to feed the figures arrived at would be the reverse of what he desired.

Smaller units such as tillers, leaves, and so on, of each species may be noted, and each class expressed as a percentage of the whole. The figure obtained for each is known as the " percentage frequency." This indicates the relative amount of each class present, and is a better index of the amount of feed available. The difficulty with this method lies in defining the unit. For example, does a stolon of a white clover plant bearing many leaves count *one*, along with the rosette of a plantain? Does the broad leaf of cocksfoot equal the small bristle blade of a fescue? Where the botanical character of the material in a quadrat is first noted and then the material is cut, collected, and weighed, accurate figures of productivity are more likely to be obtained.

A variant of these methods is to use a quadrat, say 10 inches by 10 inches, divided by cross wires into 100 squares. The top layer of the cover within each small square is noted. The figures of area covered by each species so obtained and expressed as a percentage of the total area analysed gives the " percentage area." The data collected in such a random sample is the contents of a " bird's-eye view."

Charting of the species as they occur in the quadrats, and the drawing of detailed " maps " of each sample area, enable the changes which may take place in the pasture from time to time to be followed. The areas so mapped must, of course, be marked off on the ground by pegs, or in such a way that their position and boundaries may be readily recognized in the future.

The best aspects of the "percentage frequency" and "percentage area" methods meet in the point quadrat method. Essentially this consists in lowering a series of pins point downwards from a frame on to the pasture. The pins in the frame are in line, each at a definite distance from its neighbour. The botanical nature of the first thing touched by each pin as it drops is noted. For instance, the descending pin may touch first " leaf of Italian ryegrass," or " flower of white clover," or more simply, ryegrass or

white clover. If nothing is touched until the soil is reached, " bare ground " is recorded. Thus the top cover is again recorded, but with no reference to numbers of individual plants. Hence an actively creeping leafy species will appear in the records often, though the proportion of plants present may be small. Conversely, a large number of small, unproductive plants will not loom unduly large in the record.

The value of all the methods which record the " top cover " provided by each species, rather than the volume occupied by it, derives from the fact that in a grazed pasture those species which when eaten recover first, reach the upper levels first, and therefore are recorded in much the same ratio as their ability to produce food.

The evaluation of total yield (productivity) can be based on " harvests " made periodically by running a lawn-mower over definite areas or clipping them with shears. The material so cut is collected, carried to a laboratory and there separated into botanical fractions. Each fraction can be weighed and a very accurate assessment of productivity obtained.

Enough has been said to provide an outline of the methods employed; all are laborious and require in the analyst ability to recognize at sight small pieces or units of individual grasses.

Carrying Capacity

Carrying capacity can be evaluated in terms of the number of days a pasture can feed a beast; for example, an area capable of providing feed for ten sheep for thirty days is said to have a capacity of three hundred sheep days.

The yield given by beasts grazing an area over a definite period may be taken as a measure of pasture productivity. For example, so many pounds of mutton or gallons of milk produced per acre per week might be regarded as due to the pasture. Errors not connected with the pasture enter into this class of data, for beasts vary in their ability to profit from their food.

Factors affecting the Yield of a Pasture

Of all the factors affecting pasture production, water supply is one of the most important. That this is so is well seen in a general way when the rainfall map of an area is superimposed on another

map of the same area but showing the distribution of pasture. The pasture areas tend to coincide with areas of higher rainfall. Indeed rainfall is a potent factor in determining whether the system of agriculture followed in an area is grazing or arable. It is interesting to compare the western side of Britain with the drier eastern side in this regard. If the productivity of the pastures on soils of equal fertility are considered, the better the rainfall the better the pastures is a rule quite generally followed.

Distribution of Rainfall

The distribution of the rainfall throughout the year is almost as potent as total precipitation in affecting the yield of pastures, distribution of grassland in an area, and the system of farming followed there. If, annually, dry spells of sufficient length and intensity alternate with periods of good rainfall, the yield of pasture will rise and fall. On the other hand, if the rain falls equally throughout the twelve months, the yield at different periods of the year will tend to remain constant unless conditioned by other factors such as temperature. Where supplementary feeding is not economical or practicable, the intensity of stock carried on an area must fluctuate with the rises and falls of pasture yield. In the North Island of New Zealand the rainfall in favoured areas tends to be equally distributed throughout the year, and temperatures do not reach extremes either way. In these areas the pastures remain productive all the year round. Broadly speaking, the system of farming adopted there concentrates on the production of dairy products, and the number of animals per acre remains practically constant. By comparison, in the greater part of the grazing area of South Australia the climatic conditions are more periodic with winter rains and summer drought. The head of stock carried per unit of area, based as it is on the production of fat lambs, tends to fluctuate with the yield. The lambs are dropped at the flush of the herbage in autumn and go off fat in spring. During the dry summer only the breeding stock remains.

The natural pastures to which the data pertain is typical of the better rainfall areas of South Australia. The pastures there, in the not top-dressed portions, are dominated by a perennial native grass, Danthonia, and in the top-dressed areas more by annuals. The annual yield and rainfall data are represented

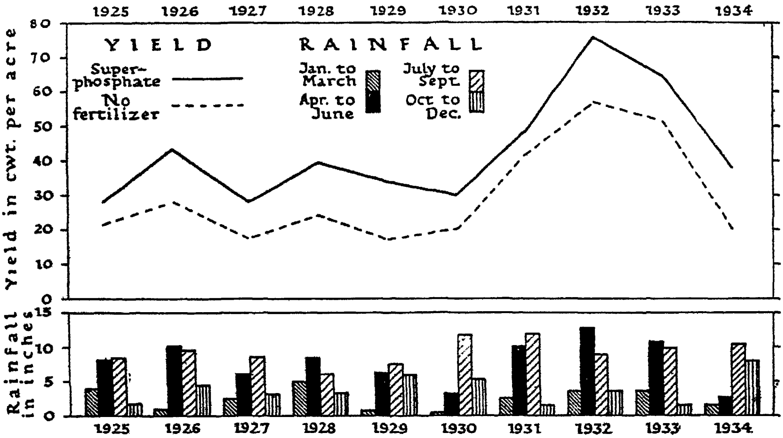


FIG. 170

Pasture Yield

Graph of the annual yield of natural pasture at Waite Institute, South Australia, together with rainfall data in quarterly periods for each year. (Superphosphate top-dressed 185 lb per acre)

(*From Trumble and Cornish, Jour. C.S.I.R., Australia 9 (1), 1936*)

graphically in Fig. 170. As regards rainfall, the precipitation in the period April-June, represented by the heavy black column, is most significant in affecting yield. In years when the grass yield is above average it is rain in the January–March (midsummer) period (depicted in the left-hand columns) which produces the extra rise. That there is a high positive correlation between pasture yield and rain falling when growth is commencing in March–April (autumn) is shown in Fig. 171. On the other hand rain in the later part of the growing period, even though it falls while plant growth is still possible, has a negative or only a slightly positive effect on yield. These details show clearly that total annual rainfall is not so important as the time at which the precipitation occurs over the twelve months. Under a periodic climate the ideal distribution would seem to be an adequate rainfall at times when the other climatic factors such as temperature permit of active growth of the herbage.

This is brought out by further work carried out in South Australia under climatic conditions similar to those detailed above, but with irrigation providing an adequate moisture supply during the dry period. In this case the monthly yield from permanent

PLA'   POTASH AIDS CLO' .RS

Left Received superphosphate and steamed bone flour *Right* Received same plus potash manure salts
(*Copyright, Messrs. Potash Ltd.*)

PLATE 74 CUTWORM DAMAGE TO PASTURE

Cocksfoot sward infected with underground grass grub

The sward is brushe(over

A "profile" of the soil below the sward to show burrow and covered "runs" on surface

(*From G. F. Hill, C.S.I.R. (Australia) Pamph. 11, 1939*)

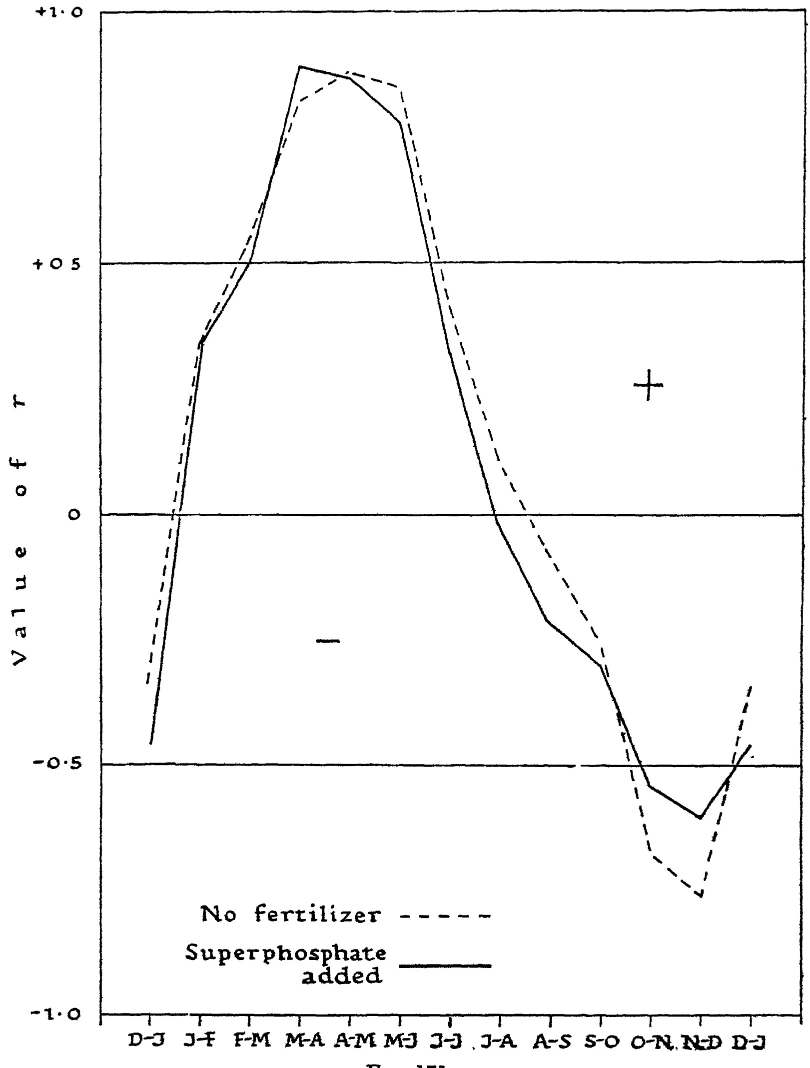


FIG. 171

Graph showing correlation coefficient (r) for the annual yield of natural pasture and the rainfall in bi-monthly periods at the Waite Institute, South Australia, 1925–1934

(From Trumble and Cornish, Jour. C.S.I.R., Australia 9 (1), 1936)

pasture follows closely the mean maximum air temperature, except in early summer, when the zenith period of yield (spring flush) of the major species comes on. These points are brought out in Fig. 172.

Over-supply of Water

In practice the converse of limited water supply is usually seen in cases of inadequate drainage. The flora in such water-logged areas is typified by the presence in the grassland of rough weed types such as rushes, tufted hair grass, buttercups, etc. Provided the soil reaction is not extremely acid, grass is often more tolerant of over-abundance of water than any other crop and does well, especially if the water is moving through the soil and not lying stagnant.

Soil Type and Pasture Production

As regards soil type it may be said that, other factors being constant, gross yield will be proportional to fertility. Only the more fertile soils can support the higher-yielding grasses and clovers. The ideal soil is probably a deep rich loam, with adequate water-supplying power. Clays often carry excellent herbage, as do many peats.

Soil Acidity and Pasture

Closely allied with questions of water supply and soil character is that of the acidity, or the hydrogen ion concentration, of the land.

One symptom of an acid condition in permanent pasture is the production of a "mat" of withered, but not rotted, plant débris on the surface layer. The presence of mat is easily felt when walking over the pasture; the effect underfoot is of treading on a thick carpet. If a turf is lifted the underlying soil has a typical musty, somewhat mouldy odour. Few earthworms live in a soil which produces a matted turf. The formation of a mat is due to the inactivity of bacteria, which in an acid soil fail to rot the dead grass leaves and other débris, so that these accumulate. The grasses and other plants which grow on such areas are usually xeromorphic in character and the predominant members of the association are bristle-bladed, such as sheep's fescue. This xeromorphic flora practically always accompanies mat, even in an area of copious rainfall. The mat acts like an overcoat and prevents rain-water penetrating to the grass roots. The water flows off over the surface and does not penetrate to the soil. Clovers, particularly white clover, are sparse or absent where a mat has developed; in fact, no creeping forms of any type

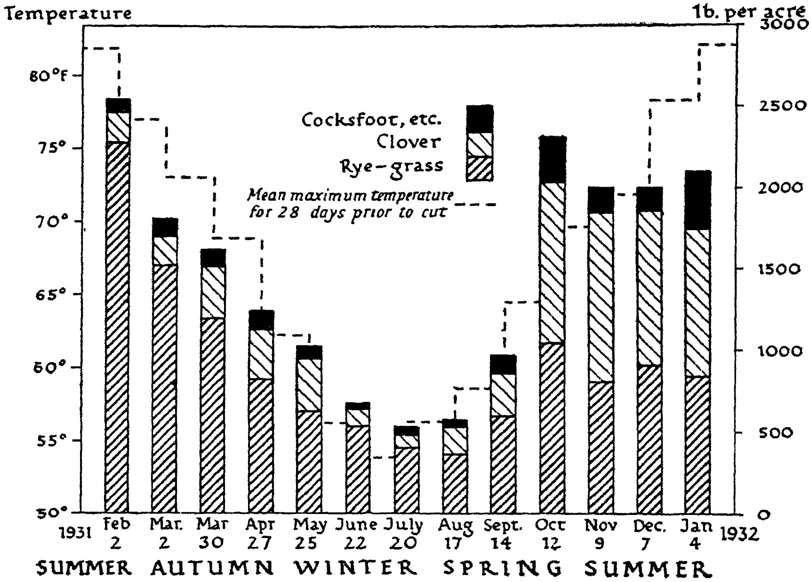


FIG. 172

Pasture Yield

Monthly yield of irrigated pasture (rotational grazing) under a climate of Mediterranean type. Note that yield follows temperature curve very closely (*From A. E. V. Richardson, Bull. 71, C.S.I.R. (Australia), 1932*)

can exploit the land. This is probably due to an inability of the adventitious roots of the stolons to penetrate through the mat. When local irrigation from a constantly dripping barrel of water soaks the mat water passes to the underlying soil. After this treatment has continued for some time, the herbage on the soaked area changes from bristle-bladed to broad-leaved types.

Flushing of Pastures

The practical use of this type of reaction is seen in areas where a spring or other natural water is available and used to irrigate or " flush " an area. That the stock appreciate the improvement in the herbage brought on by flushing is soon seen by the more intensive grazing of the irrigated areas. The concentration of livestock on the improved parts causes increased fertility of the soil. This produces an increase in the amount of good species in the turf so that coarse tufts disappear and better kinds of grass

succeed. Flushing is useful in improving small areas, but fundamentally the best method of correcting a matted pasture is to adjust the soil acidity and so promote the action of the soil bacteria.

Soil Acidity and Plant Distribution

Quite apart from this secondary mechanism through mat formation, hydrogen ion concentration affects the success or failure of herbage plants directly. Different species tolerate either acidity or alkalinity, while some seem able to exist over a wide range of *p*H values. Most pasture plants grow on soils over a fairly wide range of hydrogen ion concentration, but they each compete best at some quite well-defined level. This is well shown in Plate 72. Three different kinds of plant are illustrated, specimens of each being shown growing in a series of media extending over a wide range of *p*H values. The H.I.C. best for growth is not the same for all three plants. This difference was made clearer when in later experiments it was found that the poor growth of coltsfoot at *p*H 7·5 and *p*H 8 was due to difficulties of iron supply at that level and not directly to the H.I.C.

If the frequency with which a species occurs in soils of different H.I.C. is ascertained, not only is the range of acidity which it can tolerate defined, but the *p*H of the soil in which it competes best is established. Part of the results of a survey of meadows in Denmark are shown on page 373. Comparing two extremes, it is seen that *Deschampia* (*Aira*) *flexuosa* (wavy hairgrass) has 54 per cent. of its total occurrences in the class *p*H 3·5–3·9, and no occurrences in a class above *p*H 4·9. *Carex hirta* (a sedge) has 57 per cent. of its occurrences on class *p*H 7·5–7·9, and does not appear in a *p*H class below 6·5. *Holcus lanatus* (Yorkshire fog) is interesting in that it occurs with equal frequency over a very wide range of *p*H values. *Rumex acetosa* (sorrel), which is sometimes stated to be an indicator of acid conditions, occurs over a very wide range of acidity classes. Amongst pasture plants it is fairly safe to say that of the kinds most often included in sown swards, the grasses do best on the acid side of neutrality, but are rarely successful below *p*H 6, while clovers do best at or about neutrality or on the alkaline side of it.

The addition of lime in one or other of its forms is a prerequisite for improvement of acid pastures. Lime acts not only as a counter to acidity but as a plant food.

PH. classes	3·5 3·9	4·0 4·4	4·5 4·9	5·0 5·4	5·5 5·9	6.0 6.4	6.5 6.9	7·0 7·4	7·5 7·9	Number of occurrences
Deschampsia flexuosa	**54**	31	16	—	—	—	—	—	—	13
Galium harcynicum	**41**	18	29	5	6	—	—	—	—	18
Molinia coerulea	**26**	**26**	**26**	10	—	2	3	7	—	28
Potentilla erecta	**20**	**20**	**20**	**20**	6	4	3	8	—	39
Calluna vulgaris	**31**	24	**31**	14	—	—	—	—	—	13
Viola palustris	20	20	20	**22**	10	9	—	—	—	24
Agrostis tenuis	17	8	25	**29**	21	—	—	—	—	15
Oxycoccus quadripetatus	—	**42**	37	21	—	—	—	—	—	9
Hydrocotyle vulgaris	—	13	28	**37**	13	9	—	—	—	9
Agrostis canina	—	22	11	**38**	22	7	—	—	—	12
Festuca ovina	—	10	**32**	19	16	13	10	—	—	12
Anthoxanthum odoratum	8	8	**20**	**20**	17	14	7	3	3	46
Carex Goodenoughii	14	14	7	12	10	**17**	6	12	8	18
Holcus lanatus	—	5	14	12	**15**	12	**15**	12	**15**	55
Hieracium pilosella	—	—	27	**36**	20	17	—	—	—	10
Rumex acetosa	15	10	10	11	15	15	**16**	7	—	50
Carex panicea	—	20	10	**26**	10	10	9	9	6	24
Festuca rubra	—	7	7	**15**	**15**	**15**	14	14	13	58
Geum rivale	—	—	4	10	18	19	**22**	19	8	37
Plantago lanceolata	—	—	9	11	15	14	**23**	19	10	30
Salix repens	—	23	**34**	30	6	7	—	—	—	10
Luzula multiflora	—	12	—	**42**	24	8	—	—	17	11
Potentilla palustris	—	12	23	**36**	12	11	5	—	—	21
Galium palustre	—	—	—	13	20	**29**	18	13	6	28
Poa pratensis	—	—	—	10	17	19	20	13	**22**	35
Ranunculus acer	—	—	9	8	18	19	**21**	16	10	45
Veronica chamaedrys	—	—	—	9	19	12	**41**	9	11	14
Deschampsia caespitosa	—	—	—	4	21	**24**	14	18	19	33
Taraxacum sp.	—	—	—	17	10	6	17	**26**	23	12
Succisa pratensis	—	—	10	17	5	6	17	**44**	—	12
Cirsium palustre	—	—	—	22	16	16	**28**	17	—	21
Phragmites communis	—	—	—	—	4	9	13	**39**	35	15
Brunella vulgaris	—	—	—	8	13	23	24	**32**	—	15
Menta aquatica	—	—	—	—	5	6	17	26	**46**	11
Dactylis glomerata	—	—	—	—	7	5	26	26	**35**	15
Festuca elatior	—	—	—	—	6	4	**35**	30	26	20
Briza media	—	—	—	—	11	15	20	**40**	14	11
Filipendula ulmaria	—	—	—	6	7	27	**48**	12	—	19
Lathyrus pratensis	—	—	—	—	12	22	21	**31**	14	11
Cirsium oleraceum	—	—	—	—	—	—	29	33	**38**	19
Scirpus silvaticus	—	—	—	—	—	—	**58**	12	30	8
Trifolium pratense	—	—	—	—	15	10	14	27	**35**	8
Avena pubescens	—	—	—	**31**	9	11	23	15	10	14
Angelica silvestris	—	—	—	—	—	10	27	27	**36**	14
Carex glauca	—	—	—	—	—	14	10	**50**	26	10
Tussilago farfarus	—	—	—	—	—	7	11	**41**	**41**	9
Agrostis alba	—	—	—	—	—	—	12	24	**64**	7
Carex hirta	—	—	—	—	—	—	21	21	**57**	8

Meadow Plants. Number of occurrences in the PH. classes (per cent.)

(From Carsten Olsen, C.R. Carlsberg Lab. 15 (1), 1923)

Manuring of Pastures

It is now possible to indicate some of the reactions of the pasture to additions of the chief manurial nutrients, phosphorus, potash, and nitrogen (PKN), as they affect the botanical composition rather than the nutritional status of the pasture. While increased yield almost always follows manuring, the most striking effect of additions of these nutrients is the change they induce in the botanical composition of the sward.

Examination of the table on this page shows the effect of PKN on three different classes of pasture. It will be seen that manuring of any kind reduces the proportion of weeds, moss, and burn. (Burn consists of dead but undecayed leaves still attached to the plant.) Phosphates and potash (PK) increase the proportion of legumes present. In time the nitrogen fixed by the clover will pass to the grasses and stimulate them. The addition of a nitrogen-supplying manure depresses the clovers below the proportion in the control plot (unmanured but other-

Plot	Grasses	Legumes	Weeds	Moss and burned leafage
PKN . .	93·0	1·6	4·8	0·6
PK . .	73·7	16·9	8·6	0·8
Control .	71·7	13·1	12·8	2·4
Lowland—Permanent Pastures (average of three centres for two years)				
PKN . .	86·5	1·0	6·7	5·8
PK . .	66·8	7·2	10·9	15·1
Control .	58·2	1·7	16·3	23·8
Upland—Permanent Pastures (average of three centres for two years)				
PKN . .	91·3	4 8	3·4	0·5
PK . .	69·6	26·3	3·5	0·6
Control .	71·1	23·5	4·7	0·7
Lowland—Temporary Leys (average of two centres, one for two years and the other for one year only)				

The effect of manures on grasses, clovers, weeds, moss, and burned herbage on pastures of different types. The figures are given as percentage estimated contribution to the total herbage produced per grazing season

(*From Stapledon and Thomas, Bull. H 11, Welsh Plant-Breeding Station, 1930*)

wise treated similarly). The general principle is clear: addition of nitrogen strengthens grasses but does not benefit clovers; phosphate and potash encourage clovers rather than grasses. The balance of competition existing between the plants in the sward is altered following the application of the manures.

The extent to which these botanical readjustments between the plants proceed is roughly inversely proportional to the amount of each kind which was present before treatment. If, for example, there was little or no clover present in the original untreated sward, then the differences in clover content between treated (PK) and control are slighter.

The alterations in clover content are brought out even more plainly when the seasonal percentage-composition of the swards is ascertained. The data are represented in the table on this page. Originally in the "upland" plots there were not sufficient legumes to show a significant response to the manuring. The two "lowland" pastures, however, do show interesting results. A further point is that while white clover (the main legume involved) is seen to contribute considerably to the

		Legumes						
		May	June	July	August	September	October	Winter
Lowland pastures . .	Control	24·2	30·8	28·5	20·7	28·5	5·2	8·8
	PK	16·5	24·8	32·3	25·6	40·0	6·2	8·7
	PKN	4·0	4·7	4·7	1·0	1·5	1·0	1·0
Lowland temporary ley	Control	4·0	32·9	29·4	45·0	41·4	4·5	2·5
	PK	6·0	36·5	35·5	47·5	47·0	13·0	16·5
	PKN	2·0	12·5	7·0	3·5	4·5	1·0	2·5
		Weeds						
Lowland pastures . .	Control	8·3	9·8	8·7	5·7	14·5	7·0	11·0
	PK	8·2	5·0	5·7	3·2	2·7	4·0	13·5
	PKN	5·5	4·3	6·7	5·5	6·2	2·0	17·5
Lowland temporary ley	Control	3·5	3·0	3·0	2·0	2·5	6·5	4·5
	PK	3·5	1·5	2·0	1·0	5·0	4·5	6·5
	PKN	3·0	3·0	1·5	3·5	3·5	4·5	1·5
Upland pastures . .	Control	—	19·2	16·8	27·7	13·0	11·3	17·6
	PK	—	10·0	8·0	15·3	10 5	9·8	10·7
	PKN	—	6·8	7·3	16·8	6·3	11·2	9·7

The estimated percentage contribution of legumes and weeds to the monthly cuts and to the winter period from swards of different types under different systems of manuring. The figures therefore show relative seasonal productivity

(*From Bull. H 11, Welsh Plant-Breeding Station*)

total annual yield, it has the disability that it starts growth late in spring and falls off very steeply towards the end of September. The "miscellaneous plants" listed as "weeds" differ from white clover in this regard, for they show favourably as winter producers.

A most significant result of manuring is that the ratio alters between good grasses, ryegrasses, cocksfoot, etc., and the poorer sorts, agrostis, etc. This change favours the better kinds when these were present in the original unmanured plots in an amount sufficient to react. This is illustrated in the following table.

Species	Upland swards (3 centres)			Lowland pastures (2 centres)			Lowland ley (1 centre)		
	PKN	PK	C	PKN	PK	C	PKN	PK	C
Perennial ryegrass	1·0	Trace	—	37·4	24·4	23·9	32·9	20·3	16·4
Cocksfoot	—	—	—	3·4	2·4	0·3	35·6	28·3	26·4
Crested dogstail	6·0	1·8	2·8	18·8	14·2	11·4	Trace	0·1	0·5
Rough-stalked meadow grass	0·1	—	—	7·3	4·1	2·3	8·7	4·4	4·3
Fine-leaved fescue	32·5	33·5	25·4	4·1	3·1	2·9	0·2	1·8	2·2
Bent	35·1	20·3	20·9	7·1	8·9	10·3	0·8	0·3	2·6
Yorkshire fog	10·2	4·0	3·6	8·9	11·7	12·6	6·8	5·0	5·2

The estimated percentage contribution of individual grass species to the aggregate herbage cut as pasture for two seasons under different manurial treatments for swards of contrasting types

(From Bull. H 11, Welsh Plant-Breeding Station)

Total Yield affected by Manuring

It follows that these alterations in the botanical composition of the pasture in response to manures are accompanied by alterations in total yield, and this is exemplified in the table on page 409.

These facts emphasize that in a pasture alteration of conditions may easily favour one class to the detriment of another. The final result is often due to a change, no matter how small, which supports or encourages one competitor as against another in the constant struggle for living space. A measure of success won by one component, leading to its acquiring more room, means a greater contribution by that member to the total yield. Further, it shows that the problem of grassland management is not one of statics but of dynamics, for the pasture is in a state of constant flux influenced by the changing seasons or slight non-recurring

Subterranean Clover damaged by Lucerne Flea

Individual first leaves to show different degrees of damage

(From J. Davidson, C.S.I.R. (Australia) Bull. 79, 1934)

PLATE 76 DESTRUCTION OF LEAF TISSUE BY INSECTS

A sward showing damage by Lucerne Flea
(*From J. Davidson, C.S.I.R. (Australia), Bull.* 79, 1934)

	May	June	July	August	Sept-ember	October	Winter period
PKN . .	100	100	100	100	100	100	100
PK . .	62·7	78·3	112·6	104·3	79·1	51·4	46·1
Control .	57·7	68·6	106·3	92·2	84·0	47·7	59·1·

Lowlands—Permanent pasture (3 *centres*)

PKN . .	100	100	100	100	100	100	100
PK . .	65·0	95·8	105·3	106·0	99·9	95·2	79·7
Control .	54·2	77·0	92·7	86·0	80·9	72·2	55·7

Lowlands—Temporary pasture (1 *centre*)

PKN . .	100	100	100	100	100	100	100
PK . .	31·0	60·9	57·0	46·2	43·6	28·3	19·2
Control .	15·3	45·0	36·5	24·9	31·7	32·8	16·5

Uplands—Permanent pasture (3 *centres*)

The relative seasonal productivity of various pasture types under different manures. The yield (free of moss and burned herbage) under PKN is placed at 100 for each month, and the yield for PK and C calculated to this standard

(*From Bull. H 11, Welsh Plant-Breeding Station*)

changes in factors such as manuring. This concept of an uneasy balance between opposed members of a community should be kept well in mind in thinking of any pasture problem. Nowhere is this more true than in connection with management of grassland.

Management of Grassland

Management is a wide term, and it will receive attention under a series of sub-headings.

(1) *Biotic effect*

Often an animal depresses one class of plant in the sward and ignores the others. This soon alters the balance of competition. In this regard it is the action of the domesticated animal, grazing the herbage under man's control, that is usually referred to, but this is too narrow a view. The wild animal must be included in considering this so-called ***biotic effect***.

The well-known effect of the rabbit on pastures in Australia and members of the wild fauna elsewhere must not be overlooked. Two examples will serve here.

The Cutworm Type of Damage

The underground grass grub (*Oncopera intricata*) devastates large areas of pasture in Tasmania. This larva or caterpillar of a Hepialid moth feeds at night, cutting grass tillers at their bases and " felling " them very much as a forester might do a tree. Grasses of a tufted habit are often completely killed out by this pest, and the botanical composition of a pasture may be profoundly altered following on even quite a light attack by the grub. The grub is most active in dry seasons ; it is often drowned in wet weather. The rain which depresses the insect favours the grass, and rapid recovery of the sward results. This is especially so if the remnants of the sward left after the attack possess stolons, rhizomes, or other means for vegetative propagation. The only remedy is preventative in character, and lies in building up a sward of creeping forms so that recovery after attack is quick.

The " Leaf Eater " Type of Damage

Another wild animal of different type whose effect at first sight might be disregarded is exemplified by the lucerne flea, *Sminthurus viridis*. This small member of the Collembola abrades the surface of the leaf so as to cause wounding and the exudation of juice. The leaf soon shows white transparent areas devoid of mesophyll. In the course of a severe attack the photosynthetic area of each plant is considerably reduced. As the animal prefers legumes to grasses, this class of plant is soon depressed and grasses allowed to succeed.

Wild animals can and do cause considerable variations in the botanical composition and total yield of grassland, though perhaps not to the spectacular extent of the two cases instanced.

Domesticated Animals

The domestic animals vary very much in their effect on the sward. They have a mechanical effect. The hoof of the horse tends to cut the sward so as to leave bare patches. Horses in frisky condition, or when disturbed by flies, gallop about in a field, cutting the turf and leaving patches of bare soil, where weed seeds tend to develop. The small hooves of the sheep do not make long bare cuts or slides, but rather the cutting and treading they effect may over-consolidate a loose upper soil. Conversely the sharp edges of their hooves may break up or " mince " a mat. The degree to which either of these processes

is carried depends on the intensity of the sheep population, and how they distribute themselves over the area. Sheep tracks are commonly seen, and somewhat similar track formation due to other animals is not rare.

The profuse development of plantains round the gate of a cow paddock or behind a hedge where stock walk up and down is a frequently seen condition. Plantain seems to be one of the few plants which are stimulated by intense traffic. The distribution of the animals' droppings may not be equal over the area, and so by their manurial effect cause differences in the flora of different parts. The long grass often seen under trees where horses congregate during the heat of the day provides an example. Part of this last effect may be due to a reluctance on the part of the animals to graze the herbage of the soiled area.

Effect of Different Grazing Habits

These effects of stock are not so significant as others less easily seen and produced by the different grazing habits of the different animals. Sheep tend to eat leafage, and that of the more palatable species is preferred. Younger leaf is taken in preference to older. This is well seen when sheep are put to graze ryegrass aftermath. The flowering stalks of the ryegrass are then left growing, and tracks appear where leaves have been grazed. In a pasture the sheep tends to " punish " some species more than others. Plants of a rosette habit such as red clover with young leaf packed round the vulnerable terminal bud often suffer from this selective grazing. A highly palatable rosette plant may be completely eliminated from a pasture by the intensive grazing of sheep. Cattle, particularly when young, are indiscriminate in their feeding and tend to take herbage as it comes.

The act of grazing, too, varies with different kinds of stock. The biting or clipping action of the sheep is not seen in the cow, which on the contrary tends to grasp a mouthful and pull. The cow, particularly in a young sward, may uproot plants. A pasture grazed by the dairy cow or its followers tends to be left in a rough and tussocky condition, whereas the sheep usually leaves a close-clipped, almost lawn-like level surface.

These differences in grazing habits of the sheep and the cow are in a sense compensating, and therefore mixed grazing, preferably one class of stock following the other, is to be encouraged. The order in which the stock enters the field during a grazing

Species and strains	11/3		16/4		16/5		17/6		22/7		19/8		18/9		6/11		Average	
	Tillers	Per-cent. stem shoots	Tillers	Per-cent. stem shoots	Tillers	Per-cent. stem shoots	Tillers	Per-cent. stem shoots	Tillers	Per-cent. stem shoots	Tillers	Per-cent. stem shoots	Tillers	Per-cent. stem shoots	Tillers	Per-cent. stem shoots	Tillers	Per-cent. stem shoots
Perennial ryegrass ind.	186	0	332	0	559	45·5	282	46·2	91	3·3	129	0·8	155	0	102	0	230	12·0
Perennial ryegrass com.	321	0	162	0	559	46·3	322	45·4	79	13·9	96	1·0	193	2·6	102	0·3	229	13·7
Italian ryegrass . .	244	0	166	0	303	47·9	248	52·4	145	29·7	73	2·7	116	0	23	0	165	16·6
Cocksfoot ind. . . .	158	0	92	0	224	1·3	166	10·8	55	0	117	0	75	0	16	0	113	1·5
Cocksfoot com. . . .	128	0	117	0	172	26·7	125	8·8	44	0	79	0	58	0	18	0	93	4·4
Timothy ind. . . .	231	0	89	0	220	0	485	8·9	239	2·5	249	0	215	0	60	0	224	1·4
Timothy com. . . .	91	0	40	0	240	0	318	74·9	54	1·9	94	1·1	55	0	25	0	115	9·7
Meadow fescue . . .	105	0	83	0	280	17·2	202	35·2	48	1·2	80	0	67	0	29	0	112	6·7
Tall fescue ind. . . .	195	0	78	0	122	3·3	154	29·2	66	1·5	134	0	71	0	51	0	109	4·3
Tall fescue com. . .	132	0	71	0	315	16·2	160	23·7	69	0	82	0	80	0	87	0	125	5·0
Tall oat grass ind. . .	178	0	70	0	187	1·6	213	41·8	46	0	91	1·1	36	0	36	0	107	5·6
Tall oat grass com. .	153	0	42	0	163	17·9	128	19·5	60	38·3	26	7·7	17	0	13	0	75	10·4
Meadow foxtail ind. .	306	0	144	0	247	0·8	389	0·5	135	1·4	141	0	212	0	90	0	208	0·3
Meadow foxtail com. .	120	0	50	0	113	10·0	278	0·7	118	0·8	83	0	112	0	38	0	114	1·4
Sweet vernal grass . .	180	0	131	28·3	506	72·3	442	69·0	175	50·9	156	5·1	126	0·8	57	0·4	222	28·4
Crested dogstail . .	116	0	39	0	129	14·7	308	95·0	43	20·9	158	1·3	143	0	98	0	129	16·5
Rough-stalked meadow grass	307	0	109	0	518	2·6	667	34·4	831	0·4	580	0	242	0	252	0	438	4·7
Fine-leaved fescue . .	343	0	195	0	622	16·3	186	23·1	106	0·9	610	0	398	0	168	0	329	5·0
Average of 18 lots . .	194	0	112	1·6	304	18·9	282	34·4	134	9·3	165	1·2	132	0·2	70	Trace	174	8·2
Average 6 ind. strains .	209	0	134	0	260	8·8	282	22·9	105	1·5	144	0·3	127	0	59	0	165	4·2
Average 6 com. strains.	158	0	80	0	260	19·5	222	28·8	71	9·2	77	1·6	86	0·4	47	Trace	125	7·4

The number of tillers per sq. ft. and the percentage of stem shoots to total tillers in species and strains at each of eight cutting dates in the first harvest year. The results for the average of the indigenous and of the commercial strains are also shown
(*From Stapledon and Davis, Bulletin H 10; Welsh Plant-Breeding Station*)

PLATE 77 TYPES OF PLANT IN PERENNIAL RYEGRASS

Left to right Late flowering grazing type (S23), then late flowering pasture/hay type (S101), early flowering hay type (S24), and at right a commercial hay type (*Welsh Plant-Breeding Station Strain Numbers*)

PLATE 78 TYPE OF PLANT IN TIMOTHY (HERD'S GRASS)

Left to right Extreme pasture type (S50), a pasture/hay type (S48), specialized hay type (S51), and on extreme right a stemmy commercial type (*Welsh Plant-Breeding Station Numbers*)

period will, of course, depend on factors not botanical, but in general the dairy cow gets the first bite, followed by the sheep, then the young stock follows.

(2) *The Root-Shoot Reaction of Herbage*

How the botanical composition of a pasture will react to grazing depends on what animals graze it, and also how each of the component species react to the cutting. In the first place, grazing is equivalent to pruning and results in the kind of organic imbalance discussed under "Growth." Persistent defoliation of grasses, especially if the "stubble" is left very short, soon results in restriction of root growth and the pasture "goes back." Stimulation by additions of nitrogen to the soil causes a more or less immediate increase in leaf production, but this is slow in affecting root elongation. The carbohydrates formed in the new leaves must be worked up to nitrogenous foods, and these metabolites then moved to the apical meristems of the root before the nitrogen becomes effective in building up the plant as a whole. If the flush of leaves produced by a dressing of nitrogen is at once grazed off the roots will not benefit, and their development will be further restricted. In the extreme case, death of the plant results. The death of grass plants under close grazing is but rarely due to damage to, or removal of, the shoot buds; more usually these repercussions of shoot on root and then root on shoot are the cause. In the case of rosette plants such as red clover, death may be due to the cutting out of the buds on the very short axis.

(3) *The Tillering Reaction of Herbage*

Given that the grazing is judiciously carried out and the plant is not "punished to death," the next point lies in the kind of tillers the plant produces. In an annual plant the tendency is for most of the tillers formed to be flowering shoots. In a perennial grass, on the other hand, the majority will be vegetative and not contain a flowering head. The number of tillers an individual plant can produce is the next factor. Some kinds tiller more freely than others. These two aspects of tillering taken together determine whether a grass can recover satisfactorily from grazing or not. If a grass in face of defoliation persists in forming flowering tillers the plant will soon exhaust itself because of the drain on

its most expensive foods. Reproduction demands a high expenditure of protein which does not increase the area available for primary synthesis and replenishment of the larder. Grasses which respond to persistent grazing by producing flowering tillers soon die out. High quality of the herbage largely depends on a high proportion of leaf to stem, so the nature of the tillers produced is rendered increasingly important. The table on page 414 shows the differences in this respect between the various kinds of grass commonly included in pastures. In the table "stem shoots" are those tillers which will form flowers. Indigenous strains mentioned are specially selected lots as opposed to the normal commercial varieties.

It is to be seen that at the cutting on 11th March all species were wholly in a vegetative condition. By April sweet vernal grass was producing flowering tillers. By May all the grasses except timothy were proceeding to form flowers. Commercial perennial ryegrass and sweet vernal persisted in forming flowering tillers right through to November. In contrast, indigenous cocksfoot showed flowering tillers only for May and June; all the rest of the year the activity of the plant was devoted to leafy tiller production.

The proportion of stem tillers to leaf tillers varied enormously between species. Dogstail, for example, in June, shows 95 per cent. of its tillers stemmy and compares unfavourably with indigenous meadow foxtail, which nowhere in the table shows less than 98·6 all vegetative.

The kind of grass present in the sward, therefore, conditions to a very great extent the nature of the herbage that follows grazing or cutting. This largely conditions the ability of each grass to persist under grazing. It is this reaction, too, that underlies the difference between the aftermath or foggage from a sward of commercial ryegrass when compared with one mainly of cocksfoot. The number of flower heads in the case of ryegrass is high, while there are very few in the cocksfoot.

(4) *Nutritive Value of Pasture*

The facts noted above have a considerable influence on the nutritive value of the pasture. Young leaf contains little sclerenchyma and other fibrous elements, most of the tissues being composed of cells which are full of living protoplasm made

of protein. Of course the young tissue has a high percentage water content. The result is that young leaf shows a high yield of protein when this is expressed as a percentage of the dry matter, but not nearly so high when expressed as a percentage of the fresh weight.

(5) *Palatability of Different Components*

Chemical analysis does not cover the whole story of food value, for differences in palatability must be considered. Sheep, at least, prefer leaf to stem, and any technique of grassland management which depresses stem production and encourages leaf formation means higher palatability.

With only short periods of rest for the pasture between grazings the stem content is reduced and the proportion of leaf is increased ; hence the palatability of the fresh material and the protein content of the dry matter rises, though total yield falls. This is shown in the tables on the following page.

Indeed an authority has said : "Over a comparatively restricted grazing period the amount of the available material grazed in a series of plots of one and the same species is in inverse proportion to the gross amount of that material offering."

Differences in palatability influence the competition factor. Palatable species will be eaten to a greater extent than less palatable members of a sward, and unless there is some compensating difference in power of recovery the more desirable plants will be eliminated. The green leaf of ryegrass is high in the scale of palatability, probably second only to the leaf of red clover.

This attribute may be used in the management of the grazing of young pasture. The ryegrass, by attracting the sheep, protects other members of the sward which by reason of their slower growth would, if eaten, be eliminated by early grazing. Indeed, in a young sward, sheep are often used to "nip-back" the ryegrass which by reason of its high establishment and quick initial growth may smother the less aggressive, slower growing, but longer lasting and highly desirable components.

(6) *Effect of One Plant on Another*

The effect of one plant on another plant irrespective of a third factor which might influence the balance between them is also important, and dependent to a great extent on the habit of the plants concerned. Top grasses (tall growing) if allowed to develop

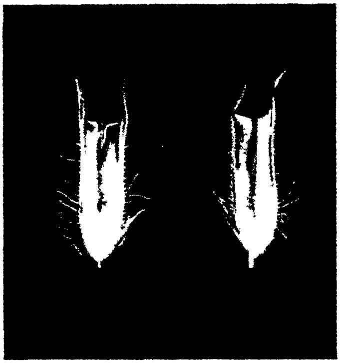
Pre-treatment before crucial date	Series	Yield before grazing	Relative yield, highest yield = 100	Yield after grazing		Amount presumably eaten by sheep during grazing period		Percent. of total herbage available eaten by sheep	
				Actual	Adjusted	By difference	Adjusted	By difference	Adjusted
Grazed monthly	B *	209	21	neg.	neg.	209†	209†	100†	100†
Grazed in Oct. and Dec. . .	D	719	71	302	103	417	634	55	85
Grazed in September . .	A	944	94	613	378	331	566	35	60
Ungrazed	C	1012	100	867	596	145	416	14	41

* Plots so closely grazed that it was quite impossible to harvest a sample after the grazing period.
† On the assumption that absolutely all the herbage on the plot was in fact eaten.

Pre-treatment of plot	Percentage of total herbage available or eaten by sheep	Relative palatability
Grazed monthly . .	100	100
Grazed twice . . .	85	55
Grazed once . . .	60	35
Ungrazed . . .	41	14

(From Stapledon, Fagan, Evans, and Milton Bulletin H 3 Welsh Plant-Breeding Station, 1927)

PLATE 79 TIMOTHY GRASS SPIKELET AND SEED



The product of a whole one-flowered spikelet to show keeled glumes with terminal awns and hair on keels

" Silver Seed," the caryopsis enclosed in the membraneous pales

' Brown Seed," the naked caryopsis, pales removed

 TYPES OF PLANT IN RED CLOVER

General view of selections at Aberystwyth. Note the very poor national strain in foreground

Three strains very different in yield and vigour. The plants in any one row are Clones

(*From Welsh Plant-Breeding Station Bulletin H 16, 1945*)

fully will always tend to smother bottom grasses (dwarfer types). The degree to which this happens depends on the proportion of top grasses to bottom grasses in the sward. If the top grasses are dense on the ground, the effect will be accentuated and may result in elimination of the bottom grasses. In this way, too, the taking of a hay crop by permitting full development of the top grasses may influence profoundly the subsequent composition of the sward. The behaviour of cocksfoot is interesting, for it does well in shade and tends to become dominant in a sward allowed to grow up and produce hay. If allowed to seed before cutting, another factor enters, and the cocksfoot is weakened by its profuse reproduction.

Ryegrasses (especially Italian) provide another case. Because of their high establishment value and ability for fast growth as young plants in the early days of the sward, they tend to oust timothy, meadow fescue, and red clover which are slower in their development. When sowing down land a balance has to be struck between the relative amount of these incompatible elements in the seeds mixture. If the ryegrass is in low proportion, the others if present in sufficient amount will be allowed to develop, and fescue at least, once established, persists long after the ryegrass is gone. The quick establishment of ryegrass, on the other hand, may provide a beneficial result. By getting above the others in the early stages it forms a " micro-climate " of higher humidity near ground level, whereby the weaker members are not dried-out in a partial drought.

Alsike and red clover rarely do well together. Whether this is due to incompatibility between them, or because they succeed best under different conditions, is not clear.

Plants Commonly used for Pasture Formation

Before considering the principles involved in the formation of a grass sward, it is necessary to know something of the plants commonly used for this purpose.

The Ryegrasses

There are four ryegrasses in commerce.

(1) *Italian ryegrass* is perhaps the most important. It is a top grass of tufted habit. In pasture it behaves as an annual, but if

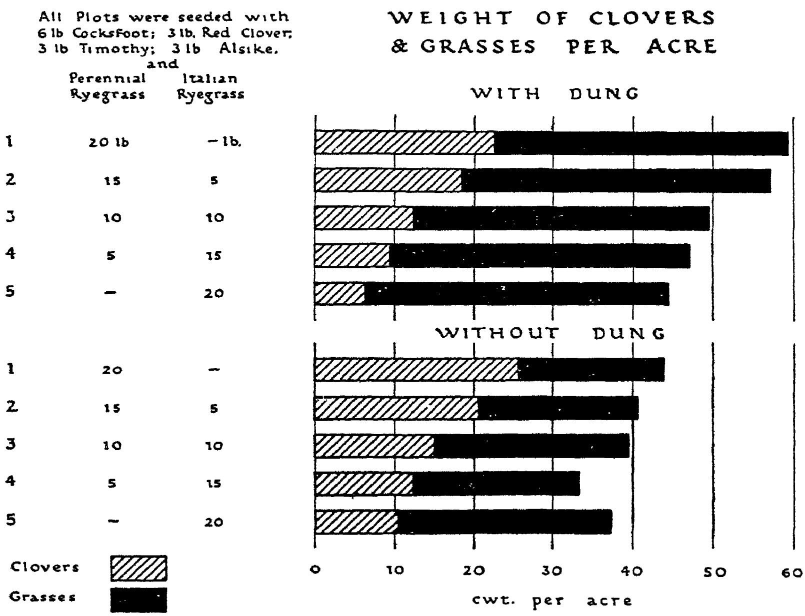


FIG. 173

Relationship between Italian Ryegrass and Red Clover
(*From Wm. Findlay, Marischal College, Aberdeen*)

judiciously grazed and flowering prevented it acts as a biennial. The most valuable attributes of "Italian" are its ability to establish quickly and then to grow during the succeeding winter. When a very "early bite" is wanted it may be provided in this way. In a mixture, Italian may easily smother out other species. When this threatens the extra growth may be "nipped back" by light grazing with sheep. This characteristic of Italian may be useful, for by growing above the other grasses it may protect them from drying winds. In order to preserve its leafiness and high palatability Italian should be grazed intermittently. It requires a good soil, and is not resistant to drought conditions except when these obtain for only a short period. Italian is sometimes sown alone to form a pure stand as a catch crop. The "seed" is large as grass "seeds" go. The bushel weights usually sold are about 20 to 24 lb., and the 1,000 grain weight is about 2 grams. Important seed sources are Ireland, Denmark, and France. No specially bred strains are available.

(2) *Western Wolths grass* is a luxuriant form of Italian ryegrass

requiring higher temperatures, more moisture, and richer nitrogen supply. Being a strict annual, it is more commonly sown in pure stand than in mixture when circumstances are suitable for its growth.

(3) *Perennial ryegrass* varies in its perenniality with the country of origin or strain. It is tufted and usually classed as a bottom grass. Like Italian it yields well in the seeding year, but does not lend itself just so well to exploitation in the first spring. It requires a reasonably high degree of soil fertility. Perennial probably " fits in " with white clover in a sward better than any other grass. The seed is as large as Italian but lacks the awn. Hence it " packs " better in a measure, and the bushel weights usually offered by seedsmen run from 24 lb. to 30 lb. When " clipped " it may go to 32 lb. or even higher. The 1,000 grain weight is about 2 grams.

There are a number of countries of origin for the commercial seed : Ireland, Scotland, Denmark, New Zealand, etc. A number of districts, as the result of natural selection, produce distinctive, leafy forms. Examples of these areas are the Hawkes Bay and Poverty Bay districts of New Zealand. A form called " Perennialized Italian " has an awned seed, and some lots at least of those which appears on the market are " cleaned out " of wild white clover.

A number of not too well defined varieties are sometimes met with under such names as Evergreen, Devonshire Eavers, etc. A form called Pacey Perennial is characterized by having "seed" of high bushel weight (30–32 lb.), which it is thought develops into a smaller, finer, leafier plant.

Perennial has been the subject of considerable artificial selection and breeding work. Strains of " hay type " as opposed to " pasture type " are now available, and if used and managed appropriately may give the grazier considerable control over the pasture as well as the promise of superior yields.

(4) *Wimmera ryegrass* is used considerably in Australia in areas subject to summer drought and winter growth period. The plant has a special use in those areas where the climate approximates to the Mediterranean type.

Crested Dogstail

Crested dogstail is a typical tufted bottom-grass. It is highly palatable and is winter green. The yield of hay is quite negligible.

The flowering stalks are practically leafless, and being very hard and fibrous, stock never eat them, so the plant commonly resows itself. The amount of dogstail in a pasture may rise steeply with the years, as some species go out and the dogstail by self-seeding replaces them. The grass is often recommended for drier situations. Here it certainly can live and persist, but for it to give its best yield it requires a reasonably fertile soil with a sufficient moisture supply. The chief use for dogstail seems to be as an alternative to ryegrass in the wetter or drier areas on land too poor or too thin to permit the more productive grass to give of its best.

Cocksfoot

Cocksfoot, often called " orchard grass " because of its ability to grow under trees, is a tufted top-grass giving high yields of hay. In pasture it requires to be well eaten back, else the plants will form coarse tufts, and a high proportion of burn will appear. This grass is long-lived, and though it may produce some feed in its seeding year, it comes to full yielding capacity only after a year or so. The yield commences early in the spring. After hay a heavy non-flowering aftermath appears which should be grazed quickly or else it becomes fibrous. The "seed" of this grass is smaller than ryegrass, and a good commercial sample will have a bushel weight of about 22 lb. From the various countries of origin, Denmark, Sweden, France, New Zealand, come lots, each of which produces plants of quite different character. These differ in amount of flowering, tillering ability, and so on. Distinctive natural strains come from special areas. For example, that from the Akaroa district of Banks Peninsula of South Island, New Zealand, is leafier and more persistent than commercial lots. The plant-breeding stations have issued specialized strains. As examples of these the S143 strain from Aberystwyth, which grows in dense broad cushions and is a pasture type, may be contrasted with S37, an erect leafy hay type from the same station.

Timothy Grass

Timothy is a perennial, tufted top-grass sometimes known as herd's grass or cat's tail. The plant is somewhat difficult to establish from seed, and does not resist competition well. It is often grown in pure stand. At one time hay composed of timothy

alone was much esteemed for the feeding of horses. The plant is winter green, and provides a fair amount of winter feed, but starts the year's active growth somewhat late. As the "seed" is small and packs well, due to the small proportion of enveloping leaves present, bushel weights are high, about 50 lb. When the "seed" is harvested fully ripe the enveloping, silvery pale falls off, and the naked brown caryopsis is exposed. A well-ripened consignment, where naked "seeds" predominate, is referred to in the trade as "brown seed," while the description "silver seed" refers to a bulk where the majority of the "seeds" remain enclosed in the silvery white pale.

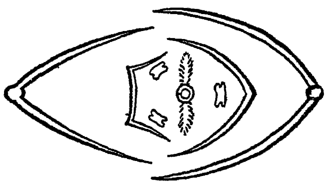


FIG. 174
Timothy spikelet diagram

Various strains of timothy are on the market. In some the selection has been towards a dense, spreading form for use in pastures; in others, the selection has aimed at a tall and leafy hay type with a yield superior to the ordinary or commercial forms.

Meadow Foxtail

Meadow foxtail is a perennial top-grass of slightly stoloniferous habit. The tillers are extra-vaginal, running sub-surface for a short distance, and then bending up to form leafy aerial shoots. The plant is difficult to establish either as a pure stand or in mixture, but once in the land in congenial situations is long-lived. This grass in Britain is one of the earliest to start growth in the spring. It flowers early, and in hay of mixed species is often past its best at cutting time. The grower tends to delay cutting until the whole of the grasses present are at their full yield. Foxtail stands frost well. It will grow in wet situations provided the water is not stagnant, and temporary flooding does it no harm.

The "seed" is light and fluffy, and samples are often much contaminated with "seeds" of tufted hair grass. Many apparently full "seeds" of meadow foxtail are really empty glumes, in which the caryopsis has been replaced by the larva of a small midge. The high price usually charged for the "seed" and the difficulty of establishing the grass tend to restrict the use of foxtail except when its success is likely.

The Fescues

The fescues used in agriculture may be classed into two groups. On the one hand there are the broad-leafed forms, and on the other hand those tending to produce leaves with bristle blades.

The Broad-leaved Fescues

Meadow fescue and tall fescue form the class of broad expanded leaved type. Meadow fescue is a tufted perennial, useful in hay and pasture. Compared with perennial ryegrass it is slower in establishing itself, and does not come into full production for two or three years after seeding. It is leafier in habit, but does not yield well in spring ; the chief contribution of meadow fescue to the pasture yield comes in summer. In the early stages of the sward it does not stand competition with ryegrasses, and when it is desired to have both ryegrass and fescue in the pasture the seeding rate of the one must be kept comparatively low and the amount of the other raised.

Meadow fescue shows a peculiar dormancy of the "seed," and germination in the soil may be delayed quite a while after sowing. The main bulk of the seed in commerce is produced in the United States of America and Denmark. In appearance the "seed," especially when clipped, is very similar to perennial ryegrass. A number of improved varieties or strains are available suited either to hay production or pasture. A dual purpose strain is S53 from Aberystwyth, which is described as primarily a pasture form, though it is capable of yielding a good late crop of hay, followed by a dense aftermath.

Tall fescue, the other broad-leaved fescue used in agriculture, is a coarser, taller form of meadow fescue, which it otherwise closely resembles. The "seed" of this grass produced in the Rhine valley develops into a rather finer plant, and is to be recommended in preference to the commercial seed from other sources.

The Bristle-bladed Fescues

The remainder of the fescues commonly sown are all more or less prone to fold up their leaves to form bristles. Sheep's fescue, red fescue, and Chewing's fescue are all used commercially in situations where better grasses might not succeed. Sheep's fescue and hard fescue are tufted, while red fescue and Chewing's fescue

are to some degree creeping. In fact, some forms of red fescue can behave as a couch-like weed. All the bristle-bladed fescues should be kept closely grazed, or else the herbage becomes quite unpalatable. A very dwarf bristle-leaved type, called fine-leaved fescue, is often used for lawn formation, though red fescue is usually preferred.

The Meadow-grasses

There are five meadow-grasses to be considered. Two are commonly used in agriculture. Of the others one is used for lawns situated under trees, while the fourth is a common annual weed occasionally used to produce a lawn in smoky towns. The fifth is used for special purposes in Canada.

Rough-stalked Meadow-grass

Rough-stalked meadow-grass is a bottom grass spreading by stolons. These by the method of their tillering, each forms a series of tufts. It is tufted and creeping, and binds a turf together. Though a bottom grass, and very useful in pasture, it may contribute quite substantially to a hay yield. It is a somewhat difficult grass to establish, but once in the sward is long-lived and a good yielder, especially in areas of copious water supply. It provides winter and spring feed, starting growth quite early in the year. The "seed" is small, and commercial bulks, which come mainly from Denmark, are rather variable in quality.

Smooth-stalked meadow-grass : Kentucky blue-grass

Smooth-stalked meadow-grass, or Kentucky blue-grass, is an underground creeper, and should be used in rotation grassland with care. It can behave as a "couch." In the seeding year it first produces small tufts which yield but poorly, and the plants are three years old before they reach their best. Once established it does well and persists even in quite dry situations, though it does not yield well in spring ; summer is when it provides its greatest yield. A great deal of the commercial "seed" comes from the United States of America.

Wood Meadow-grass

Wood meadow-grass does well in shade. The "seed" is not sown in farming practice, though it is often included in mixtures for lawn formation.

Annual Meadow-grass

Annual meadow-grass is practically a weed. Because it can tolerate the acid soils and smoky atmospheres of large towns it is often sown there each year to form lawns round buildings, etc.

Flat-stemmed Meadow-grass : Canada Blue-grass

In North America, Canada blue-grass, though not a large plant, is valued as a " volunteer " in stubble after a cereal crop, when it provides quite useful feed.

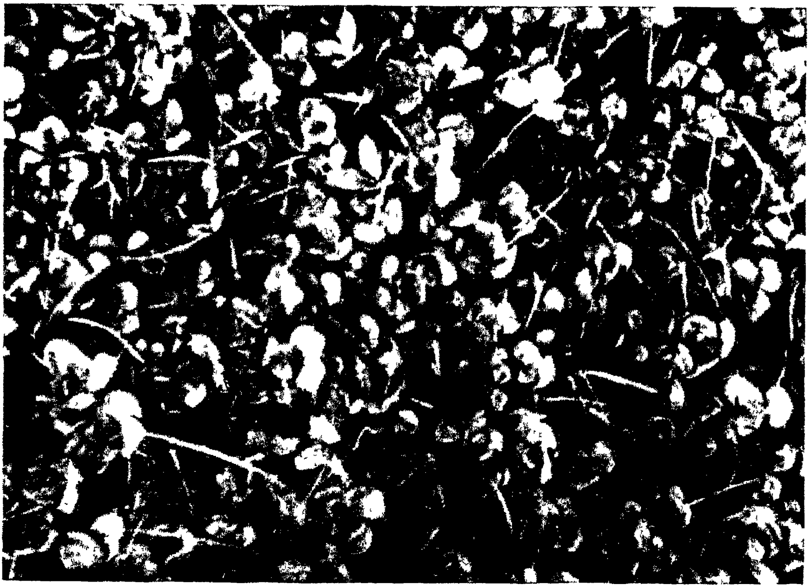
The Bent Grasses

The name bent grass has a very wide application and is attached to a number of different kinds of grass, but it should be reserved for the members of the genus *Agrostis*. The plant which originally shed some lustre on the reputation of the bents was Fiorin, a grass originally discovered in Ireland and established elsewhere by vegetative means. The grass, as introduced, was stoloniferous and probably winter green, especially in areas under a mild climate with abundant water supply. The name Fiorin to-day in practice refers to a mixture of types of *Agrostis* amongst which there are stoloniferous and rhizomatous forms. There is evidence that some of the forms which are surface creepers in wet areas are sub-surface creepers in dry areas. Indeed the members of the genus *Agrostis* provide a wide range of interbreeding genetically different types, each capable of considerable adjustment to immediate environmental conditions. The bent grasses to-day are typical of grassland on the poorer soils. In these situations, particularly when the water supply is ample, they yield quite heavy hay crops, and often produce as satisfactory pasturage as the soil permits. The " seed " is small in size, and a very little will suffice to sow an acre. Rhode Island bent, King Island bent, and New Zealand (Waipu) Brown-top are all useful ; American red-top is rather more rhizomatous and coarser in habit. Certain special strains are useful in lawn formation.

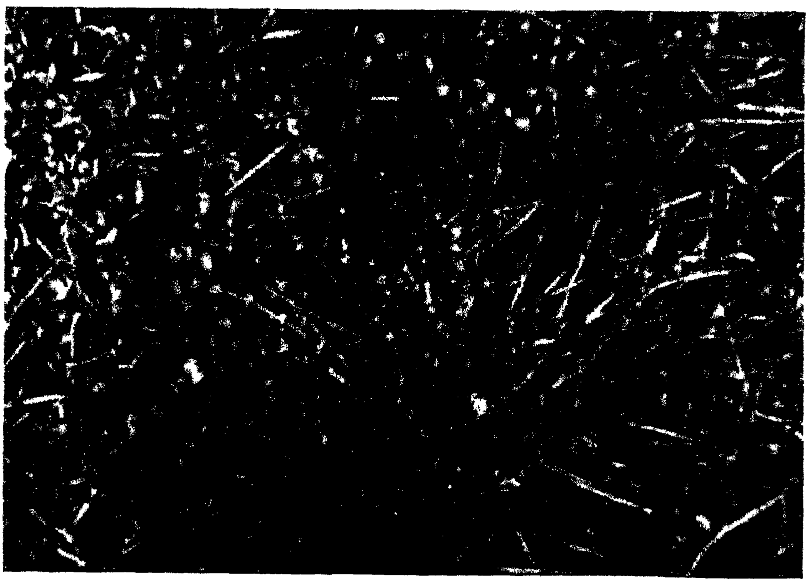
The Oat Grasses

Golden Oatgrass is a perennial bottom-grass which yields not a great deal but the produce is nutritious and apparently highly palatable to sheep. The first tillers are intra-vaginal, but later branches burst through the sheath, so that the adult plant forms

 TYPES OF PLANT IN WHITE CLOVER



S100—An improved "Dutch" or commercial form



S184—An improved but typical wild white
(*From Welsh Plant-Breeding Station Bulletin H 16, 1945*)

PLATE 82 TYPES OF PLANT IN WHITE CLOVER

Background Plants of S100 an improved " Dutch " or commercial type *Foreground* Plants of typical " wild " types

(*From Welsh Plant-Breeding Station Bulletin H 16, 1945*)

a loose tuft. It seems to do well in drier areas, but its best yield is given in regions where the rainfall is plentiful. Establishment is not good, for the "seed," though it appears quite large, is really small, being a long thin caryopsis enclosed in transparent pales. The main commercial sources of supply are France and Holland.

Tall Oatgrass, sometimes erroneously called French ryegrass, appears in two forms, bulbous and non-bulbous. In the bulbous variety the internodes situated below ground are swollen with food. The "bulbs" are thus really corms. This plant is a serious weed, and is known in some areas as onion couch or pearl grass. It should not be sown. Luckily it does not stand constant defoliation as by grazing, and therefore is easily eradicated when the land is left down to grass for a few years and kept closely grazed.

The non-bulbous form of tall oatgrass produces immense yields of leafy hay, not greatly in favour, however, as doubt has been cast on its palatability. One point in favour of this oatgrass is that its produce dries easily at haymaking.

The Brome Grasses

Different kinds of brome grass are sometimes used. Schrader's brome is sown in the hotter, drier parts of Australia. Awnless brome, sometimes called Hungarian brome, with its deep-lying rhizomes, is useful in the Central European plains. All are grasses of comparatively low yield and low feed value, useful in areas where nothing better may be grown.

Yorkshire Fog

Yorkshire fog, a hairy, somewhat creeping perennial, up till recent times was regarded as a noxious weed. Nowadays it is recommended for use on hill grazing and elsewhere where nothing better will grow. The hairs which normally cover the whole shoot are liable to cause digestive trouble in stock. In land saturated with moisture the grass becomes almost hairless, large, and leafy, and may have a decided value in such special areas.

Miscellaneous Grasses

In various countries and in special areas many grasses other than those discussed above are in use. Literature dealing with these is usually available locally, and is obtainable from the appropriate Department or College of Agriculture.

Plants other than Grasses

The clovers and other plants not grasses used to produce hay or grazing present a wide series of types, ranging from those useful only for forage or hay to low-growing, strictly pasture forms.

Crimson Clover

Amongst the clovers, crimson clover is a strict annual, producing hay which though hairy is of good quality. This plant is usually grown in pure stand and often as a catch crop. Rarely if ever is it a constituent of mixtures. A number of varieties are offered in commerce, but their relative merits have not been established.

Red Clover

Red clover is predominantly a hay plant, but may be very useful in pasture. There seems to be an antagonism between red clover and ryegrass. This incompatibility between the two hay plants arises because the red clover makes comparatively little top growth in the early part of its life, the seedling developing a deep tap-root first. If any quantity of ryegrass is present, its quick formation of ample leafage shades the clover in the vulnerable seedling stage, and so the legume dies out before it can form a proper plant.

The Major Classes of Red Clover

Many strains are in existence, each with a more or less definite country of origin. All of these are rosette plants, none are creeping. The strains available fall with some exactness into one or other of three classes : *earlies*, *lates*, and *wilds*. The late strains flower some two to four weeks after the earlies. They produce only one full crop of hay per year, while earlies produce two. This second characteristic provides the names by which they are often known. Single-cut red or single-cut cowgrass as opposed to double-cut red. The early strains often have a broader leaf, and hence are sometimes called broad-leaved reds.

The early types, possibly because of their precocious development and early, heavy yield, are in general not so long-lived as the late types. On these characteristics depend the use of one or other in agriculture. The double-cut types are best suited for

hay production and short-term leys, while the single-cut forms in general are useful for leys of two years or more.

The late types make relatively slow growth in the seedling year and flower only sparingly in the first summer ; the converse is true of the early types. Neither earlies nor lates contribute much to the winter grazing as they are then of a dwarf rosette habit. Later, in the spring, they tiller, " earlies " two to four weeks in advance of the " lates."

The " wilds," in general, provide only a poor yield of fibrous, stemmy hay. They are no longer-lived or more persistent in grazing than a good single-cut type, and hence need no further consideration here.

National Strains of Red Clover

Within these classes the yield characteristics, the persistence, and general usefulness of the strains derived from the different countries of origin vary very considerably. In general, the strains from South Europe are not so satisfactory in Britain as those from more northern areas or from home sources. North American strains tend to be rather hairy and provide a dusty hay which is not so suitable for feeding. The South American strains vary in their ability to persist and yield, and even at their best they are not so dependable as the home product.

A number of strains for special purposes are available from plant-breeding sources, and these tend to be more persistent than their commercial counterparts.

Alsike Clover

In use and habit alsike is very similar to red clover. It is reputed to be resistent to " clover sickness," and for this reason may replace red in areas subject to this complaint. The use of both alsike and red in one and the same mixture is to be deprecated unless the grower is in doubt as to which will do best in his land.

White Clover

Just as red clover is to be regarded as a hay plant, white is to be regarded as a pasture provider. There are three types of white clover : giant forms, commercial or Dutch white, and wild white. All creep by means of stolons which produce roots freely at the nodes and bear leaves on long stalks. The giant forms

have not been used much in Britain, because they demand warm, moist conditions and are not persistent in British fields. Commercial white provides the great bulk of the seed sown, for the seed of wild white is more expensive and is used rather more sparingly.

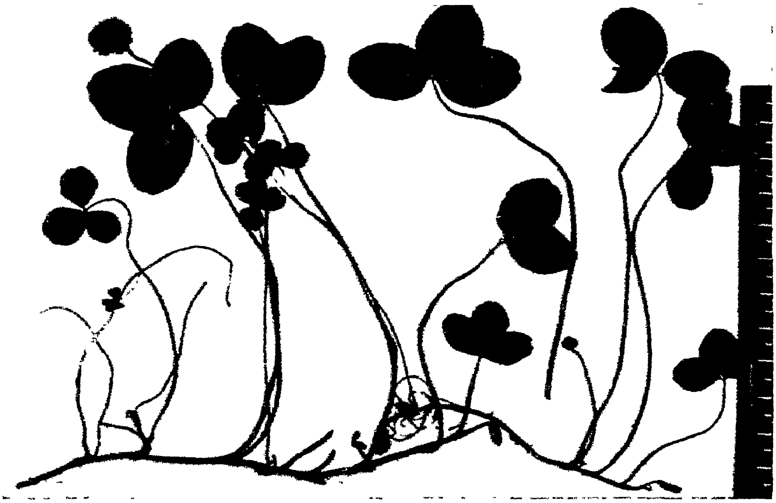
Both commercial and wild strains are alike in appearance, but the commercial strains flower more freely, are less aggressive in creeping, and are not so persistent. They form, however, a bigger plant, and so may contribute to the hay yield.

In order to encourage the production of genuine wild white and facilitate its marketing in Britain, a scheme of certification was introduced in 1930. Two types of certificate, " A " and " B," are issued. To obtain an " A " certificate the grower must produce evidence that his field has been down for over ten years, and that during that period of time no white clover seed has been sown on it. The field after passing inspection is recorded and receives a number. When the crop is harvested a sample of the seed is grown at a central institute, and if the resulting plants conform to type, the bulk receives the certificate. " B " certificates are issued similarly, except that fields of less than ten years' duration are eligible provided they were originally sown with genuine wild white clover seed. Usually the little seedlings of genuine wild white clover contain a glucoside which on hydrolysis yields prussic acid. The seedlings of ordinary commercial white contain no such compound. The test for the presence of a glucoside is easily made, and it is hoped that this will provide a method of early recognition of the two kinds.

Miscellaneous Clovers

Strawberry clover is not much used in Britain, but is valued in Australia and elsewhere. Once it is well established it yields well if the water supply is good and the soil fertility not low. It is a long, straggling plant ramifying through the sward.

Subterranean clover has proved a most valuable constituent in pasture either alone or in association with other plants. Being an annual its persistence in a field is due to its seeding habit. Any area where summer drought is acute and winter temperatures not low is a situation where this straggling annual may prove its worth.



Ladino (giant type) White Clover. (Note ruler one foot long on right)

Strawberry Clover

(*a*) The one-seeded pod of Sainfoin
(*b*) The naked true (milled) seed of Sainfoin
(*c*) The one-seeded pod of Black Medick (seed in the cosh)
(*d*) The bean-like true (milled) seed of Medick
(*e*) The seed of Lucerne. (Compare with Medick)
(*f*) The splitting fruit of Seradella (the commercial "seed" is the one-seeded segment)

There are a number of the smaller clovers more or less creeping in habit, and all treated together as suckling clover. These in drier situations often fill up "odd corners" in the pasture. They are all annuals, which by reseeding persist and may even increase in a sward. Their contribution to the green yield is not often recognized, but it may be very useful.

Leguminous Plants other than Clovers

Bird's-foot trefoil, because it commonly appears on the more acid soils, demands attention. This plant yields well in a pasture that is not too severely grazed.

Kidney vetch, a drought-resistent perennial, on the other hand seems to persist and do best on the more calcareous soils. In hay, curiously enough, this rather rosette-like plant develops in a manner very reminiscent of red clover. The tall stems then produced support a flat head of yellow flowers. These tillers, however, bear only a few leaves, and the hay is fibrous and dry.

Plants other than Legumes and Grasses

Amongst the miscellaneous plants burnet may be mentioned. This plant forms a loose rosette which, if not kept grazed in summer, throws up a long, woody stem.

The plant seems difficult to manage. In a pasture heavily grazed by sheep it tends to die out quickly. If not grazed hard it becomes over-aggressive.

Chicory is another plant of the same type. It forms a rosette, and like burnet needs careful management. It is either eaten out or tends to take command.

Initiating a New Pasture

Having now seen something of how grassland may alter in response to such variable conditions as manuring, grazing, and so on, and noted briefly some of the characteristics of plants commonly used in pasture formation, a note may be made now of the methods used in initiating a sward.

Usually a mixture of different seeds is sown, but a pasture may be established by cutting up stolons or rhizomes and sowing these. This vegetative method usually applies to a pure stand

and not to mixtures. In special cases, more often in connection with lawn formation, individual tillers are planted in rows.

Compounding a Pasture Seeds Mixture

Before deciding what species are to be included in a seeds mixture and their relative proportions, a number of questions must be answered.

Probably the first decision should be on the proportion of the grasses to clovers it is desired to have in the sward.

The period for which the pasture is going to be down will decide whether short-lived plants will suffice or if long-lived forms must be included. There is little point in including in a mixture intended for a 1–2 year ley long-lived species which come to their full yielding capacity only after two or three years. In a mixture for a long-term ley, however, a proportion of short-lived kinds must be included in order that the field may "pay its way" in the early years. In this case, when the short-lived types die out, the longer-lived forms will be established and ready to fill the vacant spaces.

The next point to decide is what percentage of the area is to be devoted to top grasses as opposed to bottom grasses. The answer to this will be affected by a decision as to whether a hay crop is to be taken in the first year or not.

Next, the proportion of creeping to tufted forms must influence the choice of species and the amount of each to be included. Both are necessary for the production of a well-knit turf.

Other factors such as the fertility-level of the soil, rainfall, the period of the year when yield is most required, the class of stock principally to be catered for, and so on, all require consideration.

Finally comes the query—are solutions to all these questions to be found by using only a few species in a simple mixture, or many species in a complex sowing? At one time complicated mixtures containing perhaps twelve or more species were compounded and sown. To-day rather simpler mixtures of as few as five or six species for the longer leys, and even fewer for shorter leys, are in vogue. It has now been realized that in the longer leys at least the effects of management, natural conditions, and manuring have a much more potent effect in determining what the composition of the sward will be after a few years than the composition of the initial mixture.

Covering the Ground

Having decided on the species which will best accommodate itself to all the various factors, the percentage of the whole area to be occupied by each is next decided. These percentage figures are then translated into units of weight (lb. per acre). Tables are published showing for each species the weight of viable seed theoretically necessary to ensure complete cover of an acre in pure stand. The amounts shown are based on the belief that in a pasture, depending on the size of the mature plants, between five and ten million individuals are required to cover an acre. These figures are now known to have little relation to practice, as the figures for establishment values on pages 390–391 show. What is usually done is that the weight theoretically required is increased by 50 per cent. for all species. This usually favours aggressive types such as ryegrass, and when ability to compete is taken into account this further depresses the balance against the poor establishers. The theoretical figures should be increased for all, but to a greater extent for the poor establishers and to a less extent for those which succeed better.

The amount of seed of each species actually ordered from the seedsman for each acre is the theoretical requirement plus an allowance for bad establishment. In arriving at this figure due allowance must be made for the fact that commercial seed is not 100 per cent. pure and all viable. The "real value" figure derived from the seed analyses of each individual component is used in this connection.

Weight of Seed per Acre

A usual mixture for a long-term ley provides some 30 to 40 lb. of mixed seed per acre. For a one-year ley the weight sown per acre is rather less. A typical mixture of this type would amount to rather less than 30 lb. per acre.

The Nurse Crop

One other botanical point must be raised. Grass "seeds" are not usually sown alone, but with or under a "nurse" crop, often a cereal. It is important that whichever nurse crop is chosen it should not shade the young grass or clovers, nor should it be liable to fall down and lodge on top of them.

The Hay Crop

The production of hay or forage is allied to pasture production in that many of the plants used in one may be used for the other. Indeed, hay and grazing are often taken in the same year from a mixture on one and the same piece of land. It should be remembered that in such a mixture a heavy hay crop is generally antagonistic to the subsequent production of the best pasture. The conditions which favour the hay-producing top grasses do not favour the dwarfer sole formers. Also the conditions set up by the hay crop within itself are quite different from those set up in a grazed sward. The competition balance struck within the two associations is quite different. Economic and other considerations often demand the violation of pure botanical principles in this regard.

Hay or Forage from a Pure Stand

Many plants when grown in pure stand yield heavy crops of hay, but are not suitable for grazing. Typical of this class is lucerne or alfalfa. As has been shown, this plant evolved in nature for life in a hot climate with poor rainfall and water only available with some difficulty in the deeper levels of the soil. When grown in a warm climate with an adequate supply of water easily available, the growth of lucerne is very fast, and three, four, or five heavy crops of highly nutritious hay may be produced by it annually. The plant is a stool-forming perennial. The fact that its seedling makes little top growth before the deep tap-root has been sent down makes the plant very sensitive to competition in the early stages. It will make a poor stand if the seed bed is not practically weed-free, or alternatively the lucerne is protected from competition by being sown in rows and periodically intercultivated. Once the root is well down top growth becomes rapid, each plant forming a wide stool, and few weeds can compete with well-established lucerne. Lucerne does not graze well, for if the " tillers " are nipped back too low the plant does not recover well.

Sainfoin, another perennial forage crop, yields heavily and grazes well. The plant is a perennial, and is available in two " strains." One of these, the so-called old common of England, is longer lived and more persistent, but gives one cut per year.

The other, giant sainfoin, does not continue to occupy the land well after about two seasons, but it provides two crops of hay, or one crop of hay followed by a heavy aftermath each season.

Many other yielders of forage might be considered. Sweet clover, a melilot, would come into this class, especially if the strains with a low coumarin content can be developed.

Lupin, too, might be considered, especially for lighter soils. This plant usually contains a bitter and poisonous alkaloid which militates against its use for forage but not for green manure. A lupin free from poisonous compounds is already extensively used for sheep feed in West Australia, and it may be expected that in Europe and America sweet, non-poisonous strains will be provided by the plant breeders.

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SECTION THREE

NEGATIVE FACTORS IN FOOD PRODUCTION

WEEDS ; INSECT PESTS ; DISEASE

THESE factors—weeds, insect pests, and disease—are competitors with, or enemies of, the green plant. They should be classed together, not just because they increase costs of production or diminish yields, but because they are inter-related and form a pattern. Weeds often provide the means whereby diseases and insect pests are harboured and carried over from one susceptible crop to another susceptible crop. Disease, by weakening the crop, often allows weeds and animal pests to get the better of it. Insects are often transmitters of disease from a sickly to a healthy plant.

By attacking one the farmer often attacks the others. Furthermore, the attitude of the farmer towards all of them is the same : the farm is to be kept clean.

The methods the farmer uses in combating these enemies are, in general, common to them all. By cultivation and manuring he strives to give the crop plant the best chance for healthy normal growth and to build up its competitive power. By tillage, the use of chemicals, and the growth of particular strains he attacks or resists the enemy. By proper nutrition, by elimination of " carriers," by prevention of infection, and the use of immunities, he protects and strengthens the desired plant population. This is the equivalent of preventive medicine in human affairs.

Once trouble appears, diagnosis and the use of appropriate remedies are called for. There is no doubt that prevention is better than cure, and the principle of sanitation or clean farming is re-emphasized. Resistance to a disease by injection or analogous treatment so commonly used in the animal world is not practicable in the plant world. Heritable immunity in plants, however, is not only possible but is a fact, and is employed more and more in practice.

In this section weeds and weed control are dealt with first. The effect of non-living external factors, such as frost and incomplete nutrition, are then considered. Next come the specific pathogens on the border line of the living, the viruses, and then finally, the organized parasites, the fungi.

Chapter XXII

WEEDS

What a Weed is

A weed has been defined as "a plant in the wrong place." This definition includes crop plants when they appear in land where they are not wanted. In an oat crop, potato plants sprung from tubers inadvertently left in the soil (ground-keepers) provide an example of such a case.

More usually, however, the term is applied to all those plants for which man has found no use and which in their evolution have developed such powers of aggression, persistence, or reproduction as to make them a menace to the best possible development of a crop. In short, this means that weeds are those plants which can compete with some degree of success against the plants specially favoured by the farmer.

The Harm Weeds Do

By their presence they decrease yields, and increase costs of production, so that both sides of the farmer's account are affected adversely. In detail weeds may produce this result in any or all of the following seven ways :

(1) By competing with the crop plant for the available living space they rob it of light, moisture, and soil nutrients.
(2) By harbouring or acting as an alternative host for virus, fungal, or insect pests they encourage attacks on the health of the crop.
(3) Their presence may reduce the value of the harvest. For example, the "seeds" of many weeds are costly to clean out of grain, wool, and other products.
(4) Many weeds contain a strong-tasting or smelling compound which communicates an unpleasant flavour to the milk or butter produced from cows feeding on the plants.
(5) The weed may contain a poison dangerous to farm animals and may even cause their death.

(6) By their presence weeds may make harvesting and other operations difficult. The presence of thistles in a corn crop is an all too well recognized case. Coltsfoot may retain moisture in the butts of sheaves to such an extent that carting of straw crops is delayed or stacks heat.

(7) Some parasitic weeds such as dodder, broomrape, or yellow rattle steal material from plants the farmer desires. They reduce yields and may weaken the crop to the point of death.

The Control of Weeds

Weed control takes two main lines of action, prevention and cure.

(i) *Prevention*

Turning first to prevention, this means simply stoppage of all avenues along which weeds may come on to the holding or spread from already infected areas.

All waste places on the farm should receive attention. Backs of buildings, stackyards, hedge-backs, and other places often neglected, should either be cleared of weeds completely, or at least the weeds cut and burnt before they seed. On the non-cultivated spots, the use of weed-killers such as waste crank-case oil, emulsified diesel oil, arsenical salts, sulphuric acid, etc., do the job cheaply and with some degree of permanence. These substances "sterilize" the soil. The oil chokes the weed if the whole plant is covered and the soil soaked. Warm weather seems to assist the action of the oil.

Neighbours may be the providers of quantities of weed seed, and any offender in this way should be invited to clear up the nuisance. Public and semi-public bodies can offend in this way. Railway and canal embankments, road-sides, rubbish tips, and other waste places can pollute the fields of a whole area. Where friendly approach and reasonable complaint made to the offending parties fail, recourse may be made to the legislation which exists in many countries whereby the obstinate may be compelled to abate such a nuisance.

All crop seeds before sowing should be tested for purity. In most countries farmers can have samples of seed tested, often for a specially reduced fee, at an official seed-testing station or agricultural institute. Seed bought through normal trade

channels should be purchased only on a declaration as to quality based on test.

Hay-loft sweepings should not be sown, for they often contain bad weed seeds. Nor should they be deposited on the manure heap, for there the weed seeds will not necessarily rot and die, but remain dormant awaiting transport on to the land. Travelling thrashing mills may carry weeds from one farm to the other. All machinery of this type should be cleaned thoroughly before passing from one holding to another. Tillage machinery may carry rhizomes and other propagants from dirty to clean land.

All these possible avenues of infection should be blocked.

(ii) *Eradication*

Once a weed has become established on the land the problem of eradication arises. This should be dealt with at an early date and seeding prevented. If the adage which says, " One year's seeding means seven years' weeding " errs at all, it is on the side of understatement.

Successful eradication consists of finding the weakest part of the life-cycle of the particular weed or weeds in question and attacking then.

Annual, Biennial, and Perennial Weeds

In this regard three general classes of weed may be recognized. These are :

(*a*) the annual weed, relying solely on seed for its spread and carry-over from year to year ;
(*b*) the biennial which builds up a store of food in its first year and flowers and seeds profusely the second ;
(*c*) the perennial using seeds for dissemination over the longer distances but relying for local spread and perenniality on a propagative organ.

The methods adopted in dealing with each of these differs. Further, methods employed in the case of arable land are not the same as those applicable to pasture land.

The Annual Weed in Arable Land

The annual is usually at its worst on arable land. The weak spot in the life cycle of such a plant is at the seedling stage. Seed

lying dormant in the ground should be encouraged to germinate at a convenient season, and then tillage operations can take care of the killing. For example, if a corn harvest can be got off the land early, immediate stirring of the soil will make many weed seeds germinate, when further cultivations may be used to uproot and kill the seedlings. Similarly, it often pays to stir the soil in springtime well before the crop is to be sown so as to allow the weed seeds to germinate. The seedlings can be killed then and the crop sown later.

The annual, often a weak plant in itself, does its damage mainly because of the large numbers present and their quick-growing habits. Masses of a quick-growing annual smother the slower-growing crop seedling. This smother action of one plant on another can sometimes be used beneficially " in reverse." This is seen when a heavy crop of peas or vetches gets above the weed, and lies on it like a blanket. When a strong-growing perennial like dock is present the method fails, for the weed grows up through the smother crop.

The two methods of cultivation and smother effect can be amalgamated when such a crop as potatoes is taken. Inter-drill cultivations in the early stages keep the weeds well in check, and then when the crop comes up it shades and smothers the later developing weeds.

It should be noted that some weed plants should not be simply uprooted, and left to die, but must be carried off the land and destroyed. Plants of groundsel if left lying will continue to flower and set viable " seed." The succulent leaves provide sufficient nourishment and moisture for their development. This is also true of ragwort and some other weeds.

Herbicides

Chemicals in the form of dry dusts or liquid sprays or colloidal sols are sometimes used to kill weeds. These are called herbicides. The different substances used differ in their mode of action. Those commonly used on vacant land, garden paths, or to form a fire-break, that is, where no plant is wanted, are such that they kill all plant life. Many of these remain in the soil for a long time, effectively sterilizing it. Those used on land carrying a crop must be " selective." That is to say, they must kill the weed while leaving the crop relatively unaffected. Further, the

chemical must not persist for long in the soil. The use of the term "selective" in this connection is hardly accurate. The herbicide in most cases is not selective; it is really the plant which selects the herbicide. Some plants, as will be shown below, hold the chemical while others do not. The so-called selective weed-killers would be more appropriately named the differential herbicides.

The mode of action of a herbicide is either to plasmolyse the cells of the weed, oxidize the substance of the plant body, poison the living tissues, by hormone action upset the plant's metabolism and growth or by direct influence on the processes of mitotic cell division cause death.

Some herbicides act in two ways at once. For example, a solution of copper sulphate sprayed on the plant may both plasmolyse and poison. Acting in any of these ways the chemical may affect some plants in a mixed population and not others.

The Basis of Differential Action

In a few cases the differentiation in action of the herbicide depends on the crop plant possessing an organ of propagation which the weed lacks. In such a case the crop plant may be adversely affected by the chemical, but recover, while weeds growing along with it are killed. The top growth of lucerne is adversely affected by oil sprays which kill annual weeds. After a time buds on the stool of the lucerne grow up unharmed. Smooth-stalked meadow-grass, by reason of its rhizomes, resists sprays of paraffin oil, which kill dandelions.

The powers of "selection" often depend on some smaller difference in morphological character between the weed and the crop. An example of this is seen when the weed is so covered with hair as to retain the herbicide, while a crop plant with smooth foliage throws off the chemical.

This type of difference may be exemplified by a comparison of wheat with charlock. The wheat plant has nearly erect leaves which have a smooth and waxy surface, and therefore do not wet easily. The growing points are well protected by clasping leaf sheaths. The charlock, on the other hand, carries its leaves horizontally; they are covered with hair, not wax, and therefore wet easily. The growing points of the shoot of charlock are easily accessible in a cluster of young delicate leaves. The axillary

buds, too, are easily reached by a liquid. When a watery solution of, say, copper sulphate is sprayed on to a mixed growth of these two plants the result on each is different. The solution which falls on the wheat runs off and cannot flow into contact with the buds. Such fluid as does remain on the waxy leaf surface forms nearly spherical drops, which cause only local damage. The fluid which falls on the charlock spreads over the leaves in a continuous film, and is largely retained. This causes death of the leafage. The spray runs into the buds and these, too, are killed.

Other classes of plant show similar differences. For example, it is little use using a water spray to attack weeds of the lily family, for they have leaves which reject the spray in the same way as do those of the wheat. Dusts too may be retained or rejected by different plants showing differences in shoot surface.

There is evidence that some plants have a physiological tolerance for some chemicals not possessed by other plants. For example, clovers seem to tolerate copper sulphate to some extent, but not iron sulphate. Charlock is intolerant of both. Hence it follows that solutions of copper sulphate may be used as a differential herbicide where these two plants are concerned.

The hormone weed-killers and those compounds which act by upsetting normal cell division also derive their differential quality from physiological differences ; some plants are affected, while others are not.

Factors which Affect Degree of Control

The amount of control obtained by use of herbicides varies, not only with the kind of weed but with other factors. The stage of growth reached by the plant when the herbicide is applied, and the environment (weather, etc.) which conditioned its development prior to application are both important. These affect the hairiness of the leaves, the development of wax on the shoot surface, and the thickness of the cuticle. In general, weeds are most readily affected by herbicides when young.

Another factor controlling the effectiveness of a herbicide is the weather at or immediately following its application. If rain washes the chemical off the leaves action may be reduced or prevented. Herbicides which act by plasmolysing the tissues may become over-dilute ; dusts may be washed off by rain falling after application. Too dry an atmosphere at or about the time of

application is not the best. This is especially so in connection with sprays which act by poisoning. The poison penetrates into the living tissues by diffusion; if the solution dries on the leaf entrance of the poison may not be so readily effected.

Adsorbed Herbicides

A number of poisonous sprays have come on the market in late years which act after being adsorbed on to the leaf. An example of this type is found in the yellow dye substance sodium dinitro-orthocresylate, marketed under the name "Sinox."

This substance exemplifies another feature also shown by some other weed killers. It is more active in the presence of an acid salt such as ammonium sulphate or sodium bisulphate. The added salt is called an "activator." Other substances which adsorb on to the leaves are becoming available, and the use of activators too will become more general.

Translocated Herbicides

Some herbicidal substances when applied to a plant not only kill the part they come in contact with, but move through the tissues to other regions. These have been called translocated herbicides. This characteristic is of considerable value in dealing with weeds possessed of an underground propagative organ, such as a rhizome, for not only is the aerial shoot killed, but the part of the plant below ground is eliminated. The mechanism of translocation is thought to be due to the "negative pressure" in the xylem pulling the chemical down through the vessels, but this theory does not explain all the cases.

Outstanding herbicides of the translocated class are the chlorates. The sodium salt is the most popular form. These salts are non-poisonous to animals, and are to be preferred on this account. When dry and in the presence of organic matter such as clothing or the plants they have killed, there is considerable risk of fire. Hence, though no precautions are necessary to prevent poisoning of stock or of the operators handling the material, considerable care has to be exercised in preventing fires. Any clothing wetted by the spray should be carefully washed before drying. Indeed, the use of protective clothing such as oilskins, is advocated. Chlorates are not to be recommended in clearing land for fire belts.

Hormones as Herbicides

Another class of weed-killer which needs mention includes the hormones or telemorphic substances. Some of these substances, it will be remembered, when offered to cuttings, etc., in very high dilution stimulate root formation. Some plants react to relatively weak solutions, others require greater concentration, while many appear to be insensitive. If the concentration of solution offered to the plant is at a level rather higher than that suited for root stimulation the plants die. And as some plants are more sensitive in this respect than others, the growth-promoting substances can be used as differential herbicides provided the strength of the solution used is just sufficient to kill the sensitive plants, and does not affect the relatively insensitive ones.

The substances commonly used as root-promoting substances are too expensive to use in the quantities required to exert a herbicidal effect over large areas of crop. Other compounds, more active in killing effect or cheaper to produce, are being introduced as differential herbicides.

Among the most active of these are 4-chloro 2-methyl-phenoxyacetic acid and its derivatives. The sodium salt applied at rates of the order of 1 lb. per acre is effective in depressing the germination and early seedling growth of corn buttercup, corn marigold, fat hen, and field poppy with no effect on cereals growing alongside. Yellow charlock is readily killed by this substance at any stage of growth from germination to flowering.

Various phenoxyacetic acid derivatives are outstanding in that they can operate through absorption at either the shoot or root. These substances persist in the soil for a few weeks, and show their effect when in a concentration of one part per million of soil solution or about 8 lb. per acre of soil to six inches depth.

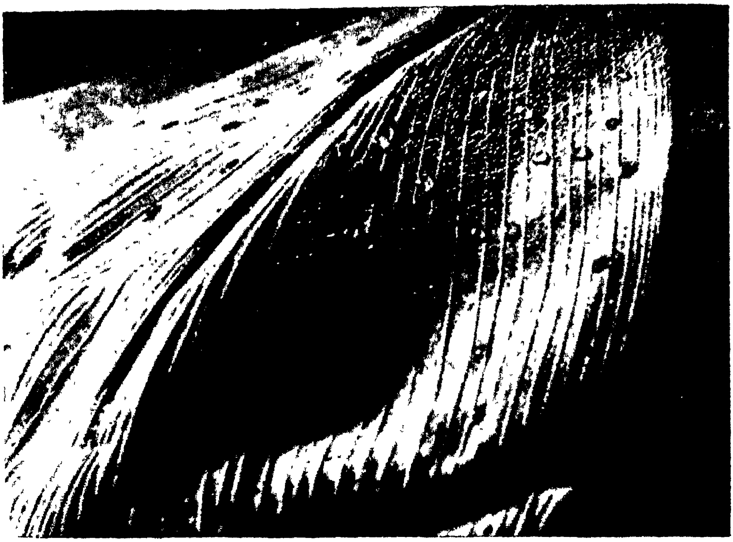
A generalization has been made that these substances are effective against dicotyledons but not against monocotyledons.

Substances which affect Cell Division as Herbicides

Substances which cause aberrations in cell division or mitosis (see p. 37) can be used as herbicides. Substances especially active in this regard, affecting some plants more than others according to the concentration used, are being discovered and made available.

The present indications are that these substances will be most

An Australian plant, the achenes of which catch on to wool, photographed on the banks of the River Tweed in Scotland. The "seeds" for this doubtless came from Australia in wool and were thrown out from the tweed mills



Leaf with waxy surface. Such fluid as is retained forms spherical drops of small area

Dock showing adventitious buds arising on the cut surface of a chopped root

PLATE 87 WEED CONTROL

A Dock plant in a crop one week after treatment with a hormone weed-killer (methoxone). The weed is now contorted and will soon die, while the crop remains unharmed (*Photo : Plant Protection Ltd.*)

In applying a differential herbicide a strip was missed. Note how in the treated portion the heavy infestation of charlock has been eliminated from the crop which remains undamaged

(*Photo : Plant Protection Ltd.*)

active against monocotyledonous plants and not affect dicotyledons. For example, iso-propyl phenylcarbamate in concentrations which killed cereals (grasses) did not affect sugar-beet, flax, rape, or yellow charlock.

Perennial Weeds in Arable Land

The same agencies as are effective in the control of annuals in arable land may be employed in the case of perennial weeds, but the way in which they are used is different. In cases where the perenniality of the weed depends on the possession of a propagant, attempts at eradication by tillage must be made with care. If the cultivating tools break up the rhizomes or other part every little piece left in the land will provide a new plant. The result will be increase and not reduction of the weed. Tillage in regard to perennial weeds should be designed to loosen and bring to the surface the organ which gives the plant its perennial character. The intact rhizomes, corms, or other propagant should then be brought together by the careful use of such implements as toothed and chain harrows. The heaps so made are then to be carted off and burnt, or heaped and allowed to rot.

On heavy land in districts where a dry autumn may be expected couch is often controlled by " killing in the clod." As soon as an early corn crop is harvested the land is roughly ploughed and then left. The clods bake dry, and the rhizomes going through them are dehydrated and die.

A plant such as dock requires special care ; the roots produce adventitious buds, and so propagate the plant. In a crop, dock should be hand-pulled if costs permit. This work is best done when the soil is wet and the tap-roots can be brought up entire.

Perennial weeds in arable land are very easily treated with herbicides of the chlorate type. These plants differ in their susceptibility to chlorates, but using the sodium salt it will be found that stinging nettles are killed with 70 to 110 lb. per acre. Coltsfoot requires rather more than this, while couch grass and creeping thistle need not less than 200 lb. per acre—that is, about $\frac{3}{4}$ oz. per square yard. Some of the more resistant plants, including dandelions, bishopweed, bindweed, wild garlic, docks, and sorrel, are killed only by applications of the order of two to three hundredweights to the acre.

The whole of a field need not be treated but only those patches

where the infestation occurs. The salt may be applied dry or in solution as convenience prompts.

If the soil is loosened a little before application of this herbicide penetration into the roots is facilitated and its efficiency improved. After killing the weed the chlorate in the soil soon changes to the chloride, and is thus rendered quite innocuous to vegetable life. About six months are required to complete this chemical change, so that land treated promptly at harvest-time is healthy, clean, and ready for sowing in the following spring.

Turnips and a few other crop plants are very susceptible to traces of chlorate but even they succeed if six months are allowed to elapse between the time of applying the chlorate to the land and the sowing of the crop.

Considerable saving in cost of chlorate can be effected if the dilute solution is placed on a cut surface. Appliances for attachment to the cutter-bar of a mower or to a scythe are available, and these deposit a sufficient quantity of solution on the stumps of the weed as it is cut.

Differential Herbicides on Arable Land

One disability of the selective weed-killers when used in a growing crop, apart from cost, is the damage inflicted on the cultivated plants by the actual operation of applying the herbicides. If more than one application is made, the amount of tramping over the crop may be considerable. This can be exemplified by reference to the use of copper sulphate on cereals. Using this salt for the eradication of charlock in oats or wheat, forty gallons of a 4 per cent. aqueous solution per acre is commonly applied when the weed is in very early flower bud. This entails getting a considerable mass of water to the field, mixing the solution, and then spraying it on.

Better destruction of the weed is obtained by using thirty to forty gallons of a 2 per cent. solution when the crop is quite young, and then giving a similar dose a fortnight later. It is necessary to apply the fluid as a fine mist-like spray and to ensure that every plant is wetted. The costs of cartage of water, and extent of the mechanical damage to the crop by tramping over it while applying these bulky fluids vary with the particular cases, but they can rarely be ignored. The more modern types of herbicides and improved spray machinery, entailing as they do smaller

quantities of fluid per acre, will be less costly to apply and cause less damage to the crop. This in conjunction with their higher degree of efficiency will favour their more extended use.

Weeds in Grassland

In grassland the annual weeds are critical usually only in the young sward. Here, if high quality seeds have been used in the sown mixture, the source of weeds must be from seeds already in the soil. The seed bed, therefore, should be made as clean as possible before sowing. If notwithstanding all precautions quick-growing annuals appear, they compete with, and may smother, the components of the mixture. Any action which penalizes the weeds—early grazing, cutting over, and so on—will allow light and air to reach the young herbage. When a mixture has to be sown on land known to be foul, alteration in the balance of the seeds mixture may be necessary, and a greater proportion of the more aggressive grasses such as ryegrass included. With annual weeds especially, the principle must be to encourage the herbage and so discourage the weed.

In a longer term ley, after the establishment stage is safely passed, the period of danger from weed aggression is when the short-lived components of the mixture are tending to go out, and the longer lived forms are hardly able to fill the gaps. Careful management and judicious manuring before and during this phase will do much to prevent weed infestation.

Another point of weakness occurs if for some reason the pasture has had to be overgrazed and becomes patchy. When this occurs weeds may gain a foothold and spread.

Once an established pasture has developed a weed flora, the method of attack varies. If the weeds are generally distributed and dense on the ground, the best answer may be to plough up and clean the land. If this is decided on, then before sowing measures should be taken to remove any condition which may have predisposed towards weed development. For example, if the weeds are rushes, buttercups, or tufted hair-grass, indicating wet, sour soil, the land should be drained and limed before resowing.

In many cases the weeds may be combated without such drastic action as destruction of the pasture. The methods to be adopted depend on the nature of the weeds. Perhaps the most

common is the type with an underground root-stock, *e.g.* creeping thistle. In this case the basic principle is clear and well understood. When the shoot of such a plant is cut back the reserves of food in the root-stock are then drawn upon to provide new aerial growth. If the new shoots are cut before they have developed sufficiently and had time to replace the reserves, then the food stores will be further depleted in another attempt to rebuild the organs of photosynthesis. This process if persisted in eventually so weakens the weed that it dies or is unable to compete with the pasture plants. The cuttings must be continued and well timed if the method is to be successful.

Bracken Control

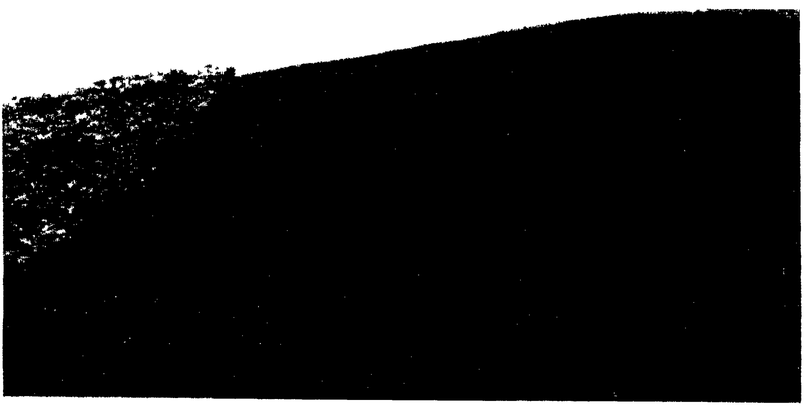
In many parts of the world probably the most intrusive perennial weed of permanent pasture is bracken. This fern is spread both by spores and actively creeping rhizomes. It rapidly colonizes any area once a foothold is gained, and by shading the grasses reduces the value of the pasture to almost nothing.

The young fronds which come up from the rhizome in spring may be eaten to some extent by stock, but unless the intensity of stock is very high this has little adverse effect on the weed. If an area is heavily stocked with cattle they break off the young developing fronds and so help to keep the plant in check. On small fields, pigs, by "rooting" for and eating the rhizomes, control the weed very well. Grazing with sheep seems to encourage rather than depress the plant.

If the fronds, particularly when young, are smashed down by rollers or cut back once, twice, or more times per year for a few years, the food reserves of the rhizomes will be depleted sooner or later, and the plant dies out. The costs of this kind of treatment are often out of proportion to the value of the land on which the bracken is growing. Where the nature of the land surface lends itself to machine treatment and hand labour is reduced costs may be less.

Sodium chlorate has proved very effective in killing bracken, especially when it is applied to the bruised or cut frond. This salt applied even to the intact leaf kills it off, and may travel back into the rhizomes and kill them also. The amount of chlorate to be used and the number and times of its application all affect the degree of success of this herbicide as a bracken killer. About

Highland steer in dense bracken. Bracken in areas suited to it is a most aggressive weed
(*Photo* : " *Scottish Farmer* ")



ELIMINATION OF BRACKEN BY CUTTING

Two photographs of the same area taken in opposite directions. (*Upper*) The plot in 1937 after its first cutting. (*Lower*) The same in 1941 with a control (uncut) plot to the left

(*Photo : K. Braid, Glasgow*)

two cwts. of the salt per acre, applied either dry or in solution in June, seems to be the most effective compromise in attaining maximum kill of the bracken with minimum bad effect on the grass growing below it. This treatment may need to be repeated in the following year.

In fields where the grass has nearly disappeared owing to the shade of dense bracken, smaller doses applied in two or three consecutive years will prove best. This progressively weakens the fern while the grass progressively thickens, and the appearance of bare ground with fear of surface washing of the soil is reduced. In otherwise inaccessible country application of the chlorate from low-flying aeroplanes has been attended by some success.

Biennial Weeds of Grassland

In regard to biennials such as spear thistle, ragwort, etc., each of which forms a rosette of radical leaves in its first year and an erect flowering shoot in the second, the principles involved are different. A positive attack may be made on the rosette stage by spudding. The flowering stage may be attacked in either of two ways : the plant may be pulled up entire or cut with a hoe or scythe at or below ground level. A walking-stick with a chisel end in place of a ferrule is useful in dealing with plants encountered casually while walking over the land. When the density of the weed is too great for these methods a mower may be used to cut the stalks just prior to flowering. This prevents further spread and weakens the plant. If cutting is repeated timeously each year any of the plants which recover and new recruits coming up from seed will be eliminated.

Ragwort may be kept down by grazing with sheep, but in recent years this has been recognized as dangerous. The plant is now known to contain a slow cumulative poison. This poison is very active against horses.

Effect of Weeds on Farm Stock

Some weeds do positive harm to stock apart from their effect on the crop or sward. There are those with hooks, awns, or spikes on the fruits or seeds which cause laceration of the mouths of grazing animals. Barleys of various sorts, by the action of the serrated awn, can cause considerable trouble in this way. Again,

the seed structures or spines borne on the vegetative parts of the plant may cause punctures in the hide and provide ingress for organisms causing disease in the animals. By causing effusion of blood and attracting the attention of blowflies harm is done. Sheep on a bare pasture sometimes " graze " gorse and blood is drawn from the skin of the nostrils and this leads to a fly " strike " on these parts.

Poisonous Plants

Poisonous plants, too, are a danger. They often cause death or disability. These may come to the stock as impurities in cakes or meals. A meal made from Java bean may contain a cyanogenic glucoside in sufficient quantity to kill as large an animal as a cow.

The farm garden may provide poisonous plants. For example, yew trees and rhododendrons are not uncommon there. When these overhang into a field or are clipped and the clippings not safely disposed of, stock may get at them with serious results. The seeds of laburnum may fall on to grassland and be picked up by stock.

Many quite common weeds contain poison, as, for example, ragwort mentioned above. Fortunately, stock do not usually eat poisonous plants found naturally in their pastures, but special circumstances often defeat this natural, protective instinct as when stock brought new into an area eat plants the home-bred animal would reject.

Ditches and water courses are usually cleaned out at a dry season of the year just when pastures are likely to be bare and burned-up. Succulent fleshy roots of plants cleaned out of the ditch in these circumstances are extremely attractive to stock. Many of the fleshy rooted plants related to the carrot and parsnip grow in ditches and are extremely poisonous. The fresh root of water dropwort is reported as fatal when consumed by cattle at the rate of 1·25 lb. per 1000 lb. body weight ; by sheep, at the rate of 0·21 lb. per 100 lb. body weight ; and by pigs at the rate of 0·151 lb. per 100 lb. body weight.

Ordinary grass may become poisonous when the flowering head is infected with ergot. The sclerotium of this fungus when present on a grass and consumed by a pregnant animal causes abortion.

Many plants are poisonous only at certain times or only in

certain organs. For example, buttercup is most virulent at flowering time. The fresh plant only is dangerous, for when it it is eaten after being dried in hay no bad effect follows.

Biological Control of Weeds

One method of attack on weeds has been left to appear as an addendum because it is rarely employed by an individual cultivator but rather by governmental authority or other agency responsible for a large area. This is the method of biological control. The essence of biological control is the discovery of a living agent such as an insect or fungus which will attack the weed and not any crop plant grown in the area. It applies most often when a weed has been imported into a new area, having left its natural enemies behind. Freed from the attacks of these natural controls the weed becomes rampant.

A spectacular example is shown by prickly pear (*Opuntia*), which was introduced into Australia as an ornamental garden plant and escaped into the wild, free from the natural enemies of its original home. It spread rapidly and overran large areas of the country.

Government decided that the problem could be dealt with only on a national basis. Soon the natural enemies of the *Opuntia* were collected overseas and imported into Australia. The release of these, particularly a moth (*Cactoblastis cactorum*), has resulted in enormous areas infested by the weed being cleared.

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CHAPTER XXIII

PATHOLOGICAL CONDITIONS INDUCED BY ENVIRONMENT

WHEN the disabilities of a plant more truly pathological in character are considered, three main classes of causative agent may be recognized. These are (*a*) factors of the environment; (*b*) viruses; and (*c*) fungi and bacteria, or other lowly plant organisms. The symptoms produced by different members of these three classes may be very similar in appearance, and considerable experience may be necessary to decide what is the cause of any particular trouble. To take quite a simple example, the brown necrotic patches produced in the soft leaves of a leek by a sharp hailstorm have been confused with lesions resulting from fungal attack or punctures made by an insect. The symptoms induced in a plant by virus are easily confused with symptoms produced by deficiency of some nutrient in the soil. Frost damage in a potato crop may simulate very closely the effect of virus. Experience in differential diagnosis is required.

TEMPERATURE AND INSOLATION

Extremes of temperature may cause pathological appearances. In hot climates "heat strain" affects many plants, and the rate of their various functions falls. This effect, attributed to the temperature, is often confused with that produced by over-intensity of light. Such a crop as coffee in many situations has to be protected by shade-trees interspersed throughout the growing area, while in glasshouse practice a coating of some form of whitewash is often applied to the glass in order to reduce the intensity of the summer sun. The usual symptoms of over-intense heat or light are "bronzing" of the leaves, a peculiar metallic appearance with brownish-purple coloration.

Low Temperature

In agricultural practice in temperate regions it is lower rather than higher temperatures that usually cause trouble. A simple

way in which this may happen occurs in winter when the soil-water is immobilized by being frozen to ice, though during the day-time at least the air conditions permit of rapid transpiration. Even leafless branches can lose a considerable amount of water through lenticels under these conditions. Thus all the symptoms of drought may appear during a spell of freezing weather.

Often it is shallow-rooted plants which suffer most. It has been shown that a plant with absorbing roots down in the not-frozen, deeper levels will continue to take in water satisfactorily. This water then moves through the upper roots unimpeded. Just as running water in a stream or pipe does not easily solidify, so the transpiration stream in the vasa passes up through the levels of the soil which are ice-bound.

Heaving

Mechanical effects of frost result in the plants " heaving." The ice expanding in the frozen earth presses the plant roots upwards into the air. When the thaw comes the soil volume returns to normal, and the upper part of the root is left partially exposed. The remainder of the root system still below the surface occupies tubular spaces in the soil. If drying winds follow the thaw the whole plant may die by drying out of the roots. Rosette plants with a conical tap-root, *e.g.* red clover, suffer most in this way.

Ice on the Surface of the Shoot

A coating on the surface of the leaves and stem may impede gas exchange and cause asphyxiation, while the sheer weight of ice and snow accumulating on the shoot may cause mechanical breaking of the branches.

Winter-killing : Frost Damage

" Winter-killing " of plants in the narrower sense of the term is due to action inside the tissues. At one time the death of cells in freezing weather was thought to follow from the expansion of ice crystals formed in the vacuoles bursting the cell-walls and protoplasts. When the drop in temperature is sudden and goes to well below freezing point, damage may be due to formation

of crystals inside the cells, but this is a rare occurrence in nature. When the onset of freezing is comparatively gradual, as is usual under natural conditions, the ice crystals within the plant occur not in the cells but in the intercellular spaces. The greater part of the water required to form these crystals must have been drawn from the vacuoles and protoplasts of the cells. Simple dehydration caused in this way may be the reason for the lethal effect of frost. Certainly the physico-chemical nature of the protoplasm is altered by freezing.

Frost Hardiness

The chief interest in these problems focuses on the fact that some plants can endure freezing temperatures and suffer no harm, while others cannot.

Plants can become " educated " to withstand low temperatures. If the drop from moderate temperatures is accomplished gradually the plant becomes " hardened." In a plant treated in this way the dry matter content rises, as does the proportion of sugars to polysaccharides. These results are probably associated with two different mechanisms. The first of these is that as temperatures fall, the rate of respiration falls faster than the rate of photosynthesis. From this a larger " net credit balance " of dry matter accrues to the plant. Secondly, at lower temperatures the equilibrium point of the sugar$\rightleftharpoons$starch reaction swings over towards the sugar side. The net effect of both these physiological responses is to increase the sugar content of the tissues as a whole, and so strengthen their ability to hold water through an osmotic mechanism.

Along with these changes in the amount and nature of the dry matter there is a parallel development of the water-binding power of the colloidal material in the plant. The result of subjecting a plant to gradually falling temperatures is to strengthen its total power to hold water against any force tending to abstract it, and this confers an increased ability to withstand frost.

Some species, varieties, or strains of plant under hardening conditions attain a greater degree of winter hardiness than do others. This is due to the fact that plants which have persisted for many generations in a cold climate have become harmonized to conditions there. Plants whose ancestors have lived always under a more genial climate and have not been subjected to the same selective influences are not so adjusted.

It is by natural selection over long periods of time that hardy and non-hardy strains have evolved. The reaction of both strains to hardening conditions is the same, though they differ in the extent to which the process can go.

The addition of soluble salts to the soil may increase the winter-hardiness of plants growing in it. This is probably due to an increase in the solute content of the cell sap increasing the water-holding power of the cells. It is to be noted, however, that over-supply of nitrogen to a plant renders it softer rather than hardier.

In the plant different parts resist cold differently. On the same plant a young leaf is hardier than an older one. The leaf bases are more hardy than the tips, while the crown of such a plant as wheat is the hardiest part of all. Thus, when frozen, the tips of old leaves die first, then the bases of the old leaf and the tips of the young leaves go, and finally the heart of the plant succumbs. The killed portions turn brown. Partial killing leaves a green centre to the plant, with the remainder brown or burnt.

Damage by Thawing

Thawing may cause damage in plants which have withstood freezing. When the thaw comes quickly crystals which have formed in the intercellular spaces revert rapidly to water. The cells appear to have neither the ability nor the time to take this fluid back into the cell, with the result that waterlogging of the tissues and rotting follow. " Blebs " or blisters full of fluid often appear in the leaf surface under these conditions. This is often seen in early potatoes frosted during the night. The morning sun beats on one side of the drills, and causes a rapid thaw on that side of the frozen plants. The leaves of the sunny side thaw quickly and are killed. The leaves on the dull side thaw more slowly, time is given to the tissues to adjust, and so they may be less severely affected.

Hail Effects

Hail, as has been said, may, by its hitting power, kill patches of tissue on soft succulent leaves.

The whole plant may be beaten down flat by hail, or by heavy rainstorms or boisterous winds.

Burning of Tissues

Drying winds often "burn" the tips and margins of leaves by excessive water-loss. This is especially so in young tissue where the cuticle is not yet sufficiently developed as to prevent the passage of water across the epidermis. Spray-laden winds blowing in off the sea may deposit common salt on leaves to such an extent that plasmolysis and death of the cells occurs.

Polluted Air causes Damage

Near large towns noxious fumes, often of a sulphurous nature, may cause death or damage of leaf tissues. Sooty and tarry smokes in the air, when deposited on leaves, reduce their efficiency. The stomata may be blocked by such solids, and definite damage or death may result. In the soil the water/air supply to the roots may be unsatisfactory, so that the living cells there do not obtain sufficient oxygen. The living roots die or are narcotized in these circumstances, and water intake is considerably affected.

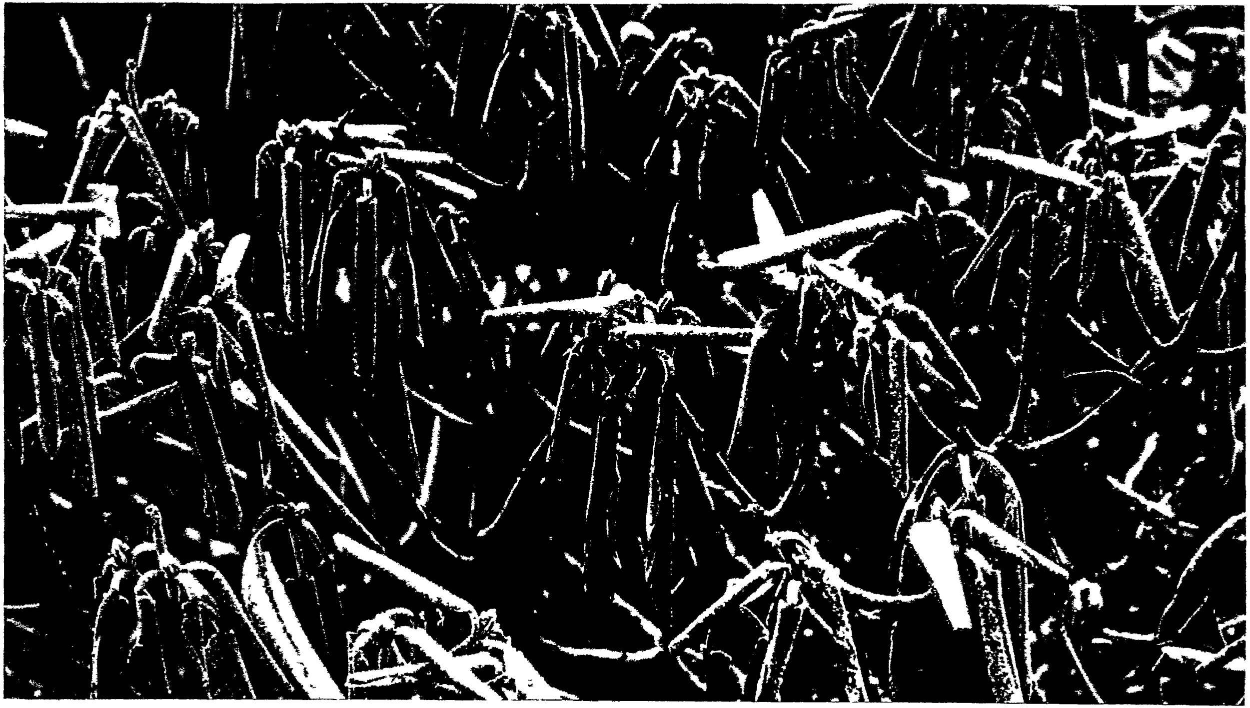
SUBSTANCES IN THE SOIL

The disabilities of the plant due to external factors so far discussed are usually readily recognized, and the cause is fairly obvious. An external factor not so readily recognized; and which produces symptoms more easily associated with other agents, is an unsuitable supply of soluble substances in the soil. The unsuitability may be due to the presence of a substance definitely poisonous to the plant. Such a case rarely arises in practice. The kind of state which commonly occurs is imbalance of the nutrient substances, which when in normal proportions are necessary for the health of the plant.

Imbalance of Salts

Imbalance may be due to simple deficiency of an essential element of either the macro or micro class. On the other hand, it may be due to an overplus of one such ingredient causing relative deficiency of another. For example, excess nitrogen may render an otherwise adequate supply of phosphorus or potash insufficient for the abnormal demands of the plant. Too much lime may accentuate a partial deficiency of boron. There is an ideal balance

PLATE 91 LOW TEMPERATURE



The leaves of an evergreen plant wilting in frost. When the temperature rises the plant will recover

The one-time burning of pyrites without control denuded this district of vegetation. Plant life is beginning to return

between any one nutrient and the others. Apart from differences in the absolute amount required, the main difference between macro and micro elements lies in the fact that the range in quantity of supply which the plant will tolerate is greater in macro than in micro elements.

The symptoms of relative over-supply or under-supply of each of the more important elements may be briefly summarized

Nitrogen

When nitrogen is deficient, apical meristems become inactive and root and shoot elongation is arrested, lateral buds remain dormant, and there are few branches. Tillering in cereals is depressed. The whole plant becomes pale yellowish-green, and later this colour intensifies so that leaves turn yellow, orange-red, or purple. Flower production is restricted. The plants generally are stunted and discoloured.

Over-abundant nitrogen, on the other hand, produces a large, soft, succulent growth, dark green in colour, and often susceptible to insect and fungus attack.

Phosphorus

Phosphorus, like nitrogen, is required for protein formation, and when deficient results in the production of a stunted plant with few branch shoots and a very poorly developed root system. The symptoms of these two deficiences (N and P) are very similar except that with phosphorus deficiency the leaf colour is a dull, bluish-green. In some cases the colour produced may resemble nitrogen starvation in being purple, but it is rarely yellowish or red. The leaf margins may show scorching in the absence of phosphorus.

Calcium

With short supply of this element the young leaves become considerably distorted, rolled, and curled-up with ragged edges. The root system is poorly developed and stumpy. In the cabbage and turnip class of plant the chlorophyll of the shoot is deficient or absent, and chlorosis is said to occur. The margins of the leaf may be quite white. Clovers and related plants are sensitive to calcium shortage. Red clover, for example, cannot take up soluble calcium from a medium of high hydrogen ion concentration (low *p*H). Legumes in lime-deficient soil show white-

spotting chlorosis, and the petioles of the leaves bend or "kink" in the middle region, allowing the blade to droop or hang down. With these plants the position in regard to this element is complicated, because the acidity-intensity of the soil (H.I.C.) affects nodule formation on the roots, and these are also concerned in the production of symptoms.

Tuberization of the potato may be quite inhibited in a soil extremely deficient in lime.

Magnesium

Plants growing in a soil deficient in magnesium show chlorotic symptoms which commonly commence in the older leaves. This symptom is probably connected with the fact that magnesium is required for chlorophyll formation, and is actually the only metallic component of the molecule. The symptoms of magnesium deficiency vary very considerably as between different kinds of plants. The members of the cabbage family seem to show the effects of shortage of magnesium before others. Cauliflower, broccoli, and kale are most susceptible. Chlorotic marbling or mottling of the leaves is a first symptom, followed later by the appearance of bright yellow, red, orange, and purple coloration.

In swedes magnesium deficiency is difficult to tell from phosphorus deficiency owing to the reddish-purple colour produced in both cases.

In potato different varieties show different detailed symptoms of magnesium deficiency, but usually these are all chlorotic or necrotic in character. It has been stated that "blight" is more severe on potatoes growing on magnesium-deficient soil. Tomatoes grown under glass are often given heavy dressings of potash. This brings on a marked early chlorosis typically symptomatic of deficiency of magnesium in this plant.

Potassium

The most obvious symptom of potassium deficiency is a scorch or burn at the leaf tip or leaf margin. The plants are stunted, and the leaf colour is a dull, greyish blue-green. The general appearance of lack of vitality in the plants is typical.

Clovers and their allies show pronounced symptoms in potassium deficiency. In addition to marginal browning, clover leaves in the early stages of the trouble show a crescent-shaped brown arc with pronounced spotting.

Sulphur

Deficiency of this element is indicated by chlorosis and browning of the leaves ; the buds die and plants are stunted. In many crops the general appearance is very similar to that following nitrogen deficiency, but in the case of lack of sulphur the roots have a peculiar brown coloration.

Iron

Iron deficiency is usually associated with high lime content in the soil, and hence the chlorosis which is typical of deficiency of iron is often referred to as lime-induced chlorosis. The excess lime present affects the rate of iron intake. In cereals, the chlorosis is often accompanied by a dying of the leaf tips.

Manganese

In oats, " grey speck disease," often mistaken for the symptoms of fungus attack, is caused by lack of manganese. Greyish specks or streaks appear on the lower half of the leaves when the plant is four or six inches high. In addition to the grey specks, the leaf doubles over with a transverse fold. The roots develop poorly.

The leaves of wheat and barley plants subjected to manganese deficiency are faintly chlorotic and may be streaked with yellow.

In crops such as kale, cabbage, and their allies, the leaf may be entirely chlorotic except for the veins, which remain green. In response to lack of manganese the condition known as " speckled yellows " appears in sugar beet. The seed of peas grown on manganese-deficient soil shows a characteristic brown spot on the morphologically upper face (inward facing surface) of the cotyledons. This condition is usually known as " marsh spot."

Boron

The symptoms produced by boron deficiency vary. Cereals seem to have a very low requirement for boron, and hence they rarely show well-defined symptoms. " Root " crops on boron-deficient soil show browning or " rotting " of the inner tissues of the " bulb."

Cauliflowers are very susceptible to a poor supply of this element, and indicate a lack by failing to develop a " curd." If the deficiency is not extreme the curd turns brown. Cabbages, curiously enough, seem to be unaffected.

An over-supply of boron can be as bad as an under-supply.

For example, in the potato, over-supply of boron may prevent "germination" of the "seed," or it may inhibit development of the sprouts and their adventitious roots.

Zinc

The leaves of maize show white chlorotic tips when grown in a soil deficient in this metal. The condition set up is usually referred to as "wither tip."

Copper

Lack of this element in the soil seems to affect the herbage growing on it less than it does the grazing animal. "Falling-down" disease of cattle in West Australia is associated with deficiency of this metal in the soil; animals grazing on copper deficient herbage when driven fall down and die.

The twigs of fruit trees growing on certain soils die back progressively from the tips; the leaves wither and die. The "disease" is known, generally, as "die-back" or exanthema, and is readily cured by injection of copper salts into the root crown or spraying the leaves with soluble copper compounds. In cereals marginal chlorosis yellowing of the blade and withering of the leaf tips is associated with copper deficiency. This, because it often appears in the first crop on heath and peat soils when they are taken into cultivation, has been called reclamation disease.

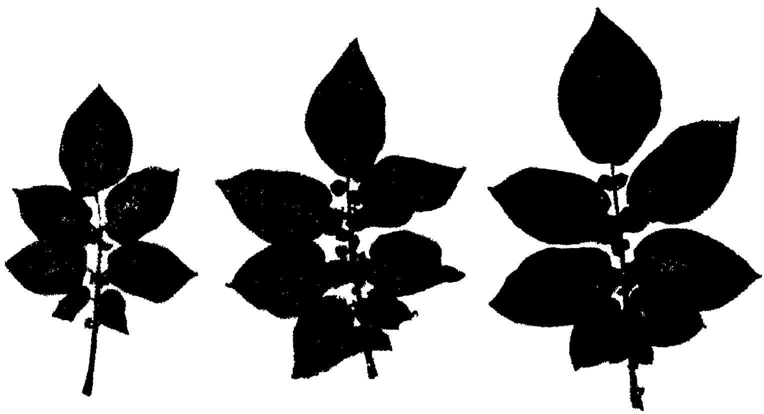
METHODS USED IN THE DIAGNOSIS OF MINERAL DEFICIENCY

From these brief outlines it will be realized that the differential diagnosis of the different deficiencies by eye judgment alone may be very difficult. Other more accurate but more laborious methods are available, a number of which may be described.

Intake of an Element through the Intact Shoot

Small plots or areas in affected crop are marked off, and watered or sprayed with a weak solution of a salt supplying one of the metals suspected of being deficient. The leaves should be thoroughly wetted. In twelve to fourteen days the plot receiving that element which is deficient in the soil will show a reduction of symptoms. The method is most successful if practised on a young crop.

(*Left*) Curling due to lack of calcium. (*Centre*) Marginal browning (burn) due to too little potash. (*Right*) A normal leaf for comparison



Balance of nutrients is as important as absolute amount. (*Left*) Leaf from a plant receiving nitrogen only—nearly normal. (*Centre*) Leaf from plant supplied with nitrogen and phosphate—note crinkle, an early symptom of potash lack. (*Right*) Leaf from plant given all three nutrients—normal. All three plants otherwise treated alike

(*Photo : Potash Ltd.*)

PLATE 94 BIOLOGICAL ANALYSIS FOR MAGNESIUM

(0–300 = Mg supplied in μg per 50 ml.)

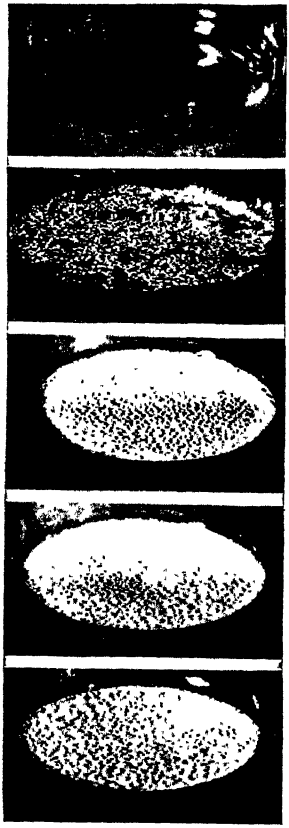
0 No development

25 Slight growth of sterile mycelium

50

75

100



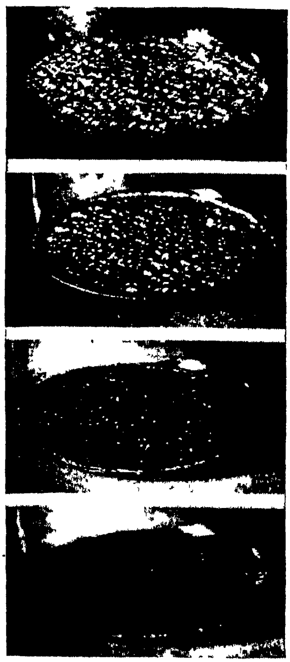
Sterile mycelium becoming increasingly strong, from 50 to 100 μg Mg per 150 ml.

150

200

250

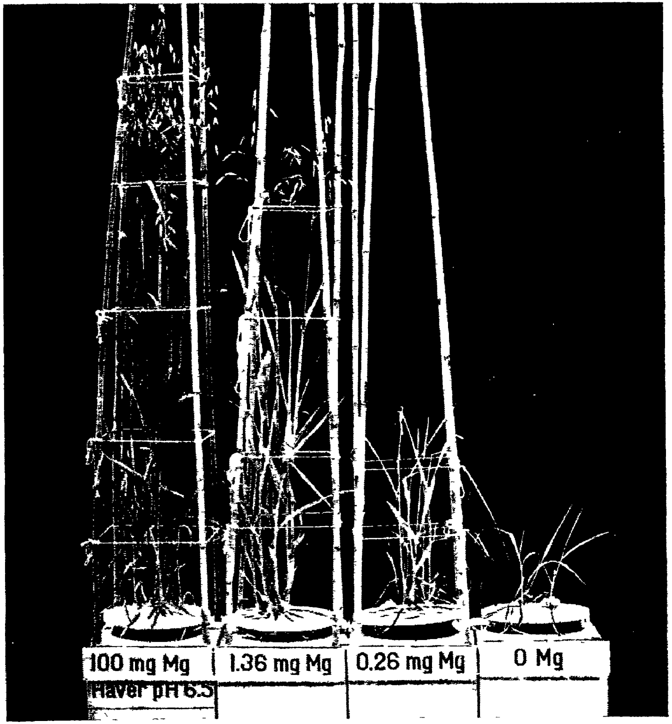
300



Production of black spores commences with 150 μg Mg per 50 ml. and increases with each increment of the nutrient. (Above 400 μg no further changes in the mould appear)

Growth of a common mould (*Aspergillus niger*) on a complete nutrient medium except for magnesium supply

(*From J. Smit and E. G. Mulder, Holland*)



The effect of paucity of supply of magnesium. (*Left*) Oats in a water culture complete except for variations in magnesium supply. (*Right*) Leaves from plants one week after 3 mg magnesium per litre had been added (*From J. Smit and E. G. Mulder, Holland*)

Chlorosis in Peach

The twig has been injected with a 0·1 per cent. solution of ferric chloride. The topmost leaves are recovering their green colour in response to the supply of iron (*Copyright, East Malling Research Station*)

Marsh-spot in Peas

A pea seed split to expose inward aspect (upper surface of cotyledon). Note the brown necrotic area

Injection into the Leaf and the Stem

With fruit trees, a test may be made by cutting off a leaf-tip under a weak aqueous solution of an appropriate salt as described on page 308. The solution will be pulled into the leaf, and a local diminution of symptoms will appear in a few days.

Injection into the trunk of the tree by the methods described on page 310 will also produce significant effects when an appropriate solution is used. Injection methods are now being advocated, not only for diagnosis, but for " feeding " the tree.

Indicator Plants

The use of indicator plants for testing soil has been suggested. For example, on a soil suspected of manganese deficiency oats may be grown, and the typical grey speck will appear if the element is really in short supply.

Marrow-stemmed kale, broccoli, and cauliflower all will show very characteristic symptoms when grown in soil deficient in nitrogen. In agricultural practice, the troubles arising from an imbalance of nutrient supply usually arise in a commercial crop when there is little time for elaborate testing if the crop is to be saved and a normal harvest secured. If the trouble is noticed soon enough, that is, when the crop is young, manurial dressings of an appropriate mixture of salts may be applied. Once the deficiency has been accurately diagnosed, the manuring programme for the future should be suitably modified.

When the symptoms of deficiency diseases are compared with those due to the presence of a virus, it will be seen that differentiation in diagnosis between the two classes of cause may be as difficult as between two deficiencies.

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CHAPTER XXIV

PATHOLOGICAL CONDITIONS INDUCED BY VIRUS

DISTINCTION between a deficiency condition and a virus disease condition lies not so much in the actual symptoms exhibited by the affected plants but in the fact that, if the cause be a virus, the trouble may be transmitted from an unhealthy to a healthy plant. The methods adopted vary. Some cases require the normal, healthy plant to be grafted on to the unhealthy one. In other cases simple inoculation of the healthy plant with sap from a virus-infected individual is effective. If the cause of ill-health is due to a deficiency of an element the healthy plant will remain healthy no matter what method is used. Virus is transmissible, deficiency is not. Deficiency is readily diagnosed and cured by the use of an appropriate salt solution or manurial treatment. Virus symptoms in general do not answer to treatment.

WHAT A VIRUS IS

The plant viruses are best known from their effects on the plants which they attack ; none of them has ever been cultivated outside the plant body. They are not visible in a microscope using visible light, for their structure is ultra-microscopic. Some viruses have been isolated from the host, and all have proved to be some form of nucleic acid ; they are of the nature of nucleoproteins. These extracted " chemicals " may be stored outside the plant and retain their virulence for varying periods. The viruses then may be defined as pathogens, always parasitic, and composed of units ultra-microsocopic in size. Viruses being parasitic in nature, a plant which bears them may be called the host.

SYMPTOMS OF VIRUS ACTION

The symptoms of attack by virus are very variable, for the appearances produced depend not only on the nature of the virus but on the nature of the host. The commonest type of symptom is a deformation of the shoot, a crinkling and rolling of the leaves, more generally distributed over the plant than is seen in fungal

attack. These malformations are often accompanied by discolorations of the leaf and stem.

The same virus may cause quite different symptoms in different plants, and indeed in different varieties of the same plant, while different viruses may be the cause of identical symptoms in one host.

A plant may be fully infected with a virus and yet show no obvious symptoms. Such a plant is known as a "carrier," and it is fully capable of infecting a susceptible neighbour. The fact that the virus is present in a "carrier" can only be demonstrated by transmission experiments.

Symptoms of some viruses in certain hosts may not be visible externally, but various bodies may appear in the host tissues. These bodies may appear as crystals or simulate such lowly organisms as amœba. The tissues of the plant may be altered. For example, the chloroplasts may be damaged or reduced in number, or necrotic lesions appear in the phloem.

Symptoms of first or primary infection with virus always show in tissue developed after infection. The trouble seems to spread through the host from a centre at the point of entry to areas where growth is active, and all tissues developed thereafter show the symptoms, while older organs remain normal.

When a propagant such as a potato tuber contains the disease the whole plant developed from it shows symptoms; this is not primary infection.

Methods of Transmission

Once inside a congenial host-plant the virus increases and moves about the plant body very much as food metabolites do. The sap is now infective and may be carried from one plant to another. A diseased plant rubbing against a healthy one with very slight bruising of each may serve. The hands of a worker touching a diseased plant can carry the pathogen to a healthy one touched subsequently. A plant parasite such as dodder acting as an organic link between two plants can provide a channel for the virus.

The Insect Vector

It is an insect, however, which is most commonly the carrier of infection. If an appropriate insect sucks fluid from the tissues

of a diseased plant and then proceeds to a healthy individual, it regurgitates into the second, and so infection is spread. The more mobile the insect the greater the rate of spread. It should be remembered that small insects which are themselves but weakly mobile, may be carried great distances by wind. Any agent, insect or not, capable of transmitting the virus is called a *vector*. A quite sparse infestation of an insect, not serious as a pest in itself, may be amply sufficient to transmit virus quickly from plant to plant.

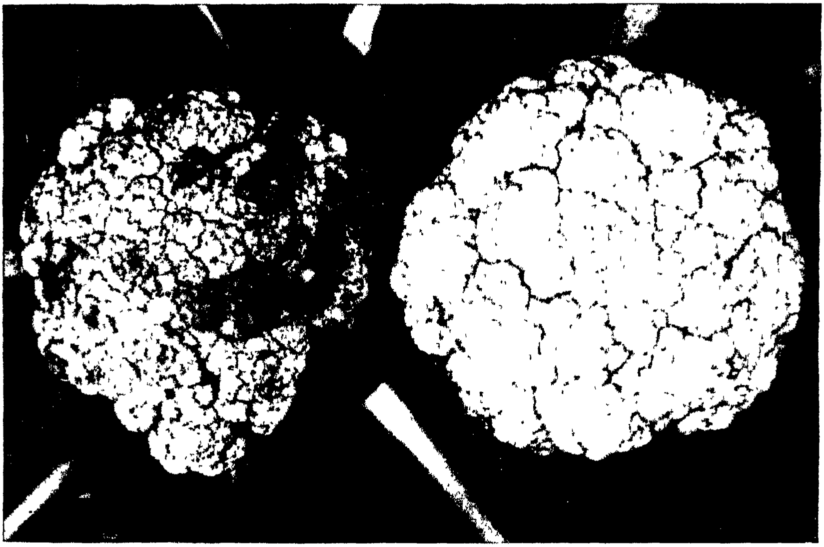
In some cases at least the insect vector does not act simply as a transmitter. Evidence is accumulating that while the virus is in the insect it undergoes some change or multiplies. Thus, while in many cases an insect which has fed on a diseased plant is immediately capable of infecting a healthy one, this is not necessarily so ; a certain period of time may have to elapse between the two incidents for transmission to be effective.

Control of Virus

Control of virus disease takes two lines : prevention and cure. Prevention depends for success on commencing with a healthy stock of plants. This attended to, any source of virus infection existing in the neighbourhood should be eliminated. Weeds often carry virus. If complete elimination of infected plants in the vicinity is not possible, the vector should be eliminated or its movement prevented.

It is doubtful if the embryo in a seed can carry virus, though it is believed that " bean mosaic " is transmitted in this way, and quite a number of cases are known where the coverings of the " seed " carry disease. The very young seedlings developed from these seeds are quite healthy, though a suspicion exists that infection of the plantlet takes place after germination, the virus passing from the covering to the emerging axis. Even a few unhealthy plants produced in a crop in this way are dangerous, for they act as sources for the primary infection of the healthy members.

A propagant taken from a diseased plant is almost certain to be infected. Potato tubers, sugar-cane sets, strawberry runners, or raspberry off-sets are all highly dangerous if derived from diseased crops. A partial safeguard lies in obtaining such propagants only from a healthy crop growing in an area where the



(*Left*) Curd showing surface browning. (*Right*) Normal

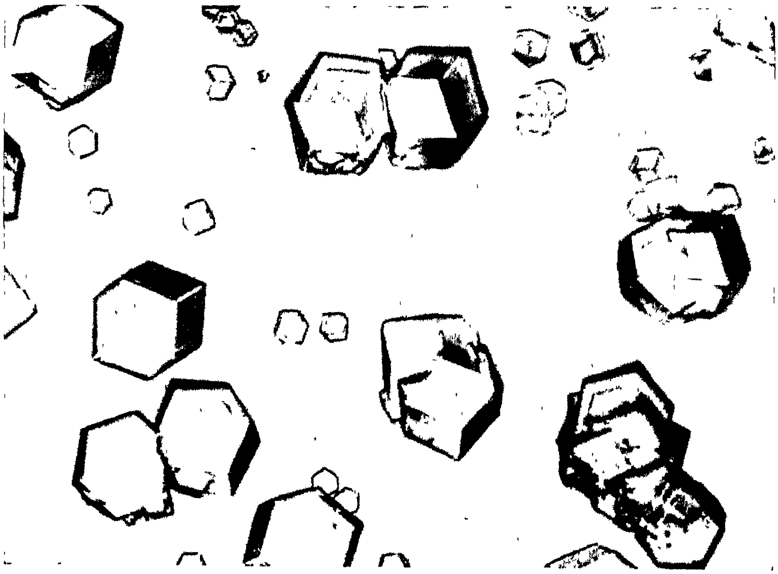
In slight deficiency (imbalance) the brown coloration appears. In greater imbalance the tissues of the stem are affected (right). In extreme cases the curd or head fails to develop

THE SYMPTOMS OF BORON DEFICIENCY IN CAULIFLOWER
(*From C. H. Dearborn, Bull. 778, Cornell Univ. Agric. Expt. Stn., 1942*)

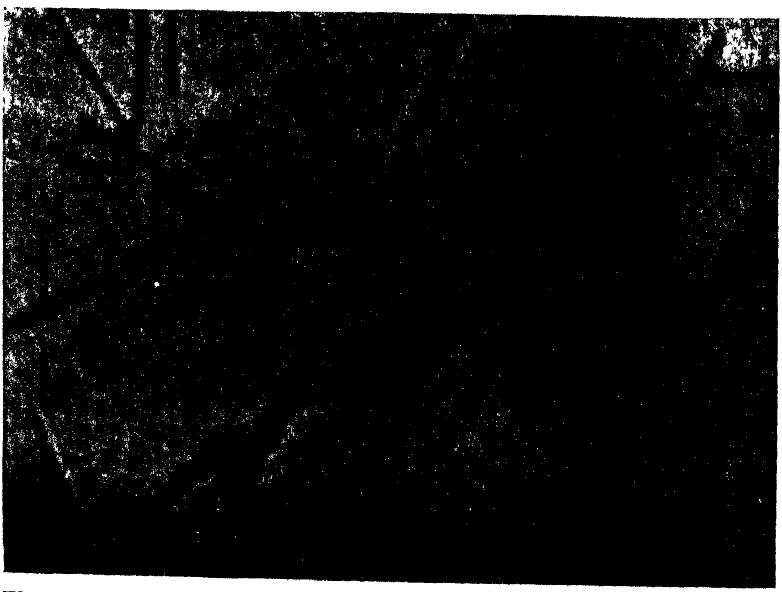
(*Upper*) Exanthema in a Pear Tree. See Plate 99. (*Lower*) Diagnosis by spraying rows of plants. Cross sprayed—the tall patches received 1 per cent. manganese sulphate (*Copyright. East Malling Research Station*)

Twigs of Pear : left to right progressive stages from exanthema to normal

Leaves of exanthemic Pear. This disease is cured by injection or supply of copper
(From J. Oserkowsky and H. E. Thomas, Plant Phys. 13, 1938)



Crystals of tomato bushy stunt virus produced by slow precipitation with ammonium sulphate in the cold



Electron micrograph of a dried film of purified tobacco mosaic virus to show the rod-like particles of various lengths (× 28,800)

(*Photos copyright, Rothamsted Experimental Station*)

appropriate vectors are scarce. This does not provide absolute protection, for a crop inspected early and certified as clean may have become infected late in the season. In this case the plants would not have had enough time to develop observable symptoms when inspected. This may be guarded against by growing a representative sample of the propagant in a glasshouse well before the main bulk is due to be planted in the field. This is done in the production of " élite " stocks. In practice, for commercial purposes, the purchase of seed from a crop proved free of disease by inspection at various times in the growing season should be adequate.

Sources of Virus for Primary Infection

Weeds in an area often maintain a " reservoir " of disease ready to act as a source for the primary infection of a crop. Not only those weeds botanically related to the crop should be regarded as suspect, but any weed should be mistrusted. One and the same virus may live and develop quite well in two very dissimilar hosts—*e.g.* tomato and chrysanthemum, or potato and aster. So too, as has already been said, some plants, weeds or otherwise, tolerate the presence of a virus but show no symptoms. These are quite capable of supplying material for the infection of a susceptible neighbour.

Prevention of Transmission

So much for elimination of sources of primary infection ; the alternative is prevention of transmission. This is usually difficult. The most obvious step is to clean up the breeding ground of such common vectors as greenfly, capsid bug, etc.

Where practicable, sowing the crop earlier or later than usual may " dodge " the incidence of the insect. Valuable horticultural subjects, or élite stocks of more humble plants, may be protected from the vector when grown under gauze screens, or grown in remote areas which are free from infective material or vectors. In horticultural practice the human hand, pruning knives, seed boxes, or roots and plant debris in the soil can act as vectors. Appropriate forms of control, as by systematic washing of the hands, disinfection of knife blades, heat treatment of boxes and soil, should be introduced.

Cure of Virus Disease

Curative measures applied to a virus diseased plant are not likely to prove feasible in general agriculture. Various chemicals have been suggested as active against virus, but their use is hardly practicable.

Heating infected plants, especially when they are in a dormant condition, promises well as a method of cure in a limited number of cases. A number of quite serious viruses are reduced in virulence or " killed " by a temperature which does not harm the plant. In other cases the virus remains unaffected by temperatures which kill the plant. Stocks or scions of fruit-trees, and in other crops propagants such as tubers, bulbs, or corms may be treated in this way.

Immunity to Virus

The breeding of varieties immune to all kinds and strains of kinds of virus is an ideal which, probably, never will be attained, though resistance to some is possible. Two forms of immunity can be recognized : conferred immunity, and inherited or genetical immunity.

The outstanding success so far in breeding for virus immunity has been achieved in Java, where the P.O.J. varieties of sugar-cane are resistant to " sugar-cane mosaic." Such plants become infected but show no symptoms and produce a full yield. They behave as carriers, however, and can transmit the disease to susceptible varieties. Varieties which tolerate the presence of a virus in this way may be a menace to the agriculture of an area. Unless they and they alone are grown in any one isolated situation, they act as a reservoir of infective material, and a supply of the pathogen is available to all susceptible varieties growing near by.

The matter does not end here, for, as has been shown, one and the same virus may infect a number of hosts otherwise unrelated. Hence, the presence of such a non-susceptible variety of one crop may result in disease attacking a different crop cultivated in the same area.

High Susceptibility to Virus

Paradoxically, it may be that the best control may come from the production and cultivation of highly susceptible varieties, and this for either of two reasons.

If a highly susceptible variety is grown the " seed " crop can be " rogued " (see p. 524) very efficiently. Any member becoming infected shows the symptoms quickly and clearly, and so is soon eliminated.

Hypersensitivity to Virus

Some varieties are so susceptible to virus that as soon as primary infection takes place the tissues round the site die. In these cases death of the tissues results in either the death of the pathogen or inability of the virus to diffuse out to other parts. In these hypersensitive forms primary infection results only in local lesions, and the trouble does not affect the plant generally.

In addition to these aspects of inherited immunity and/or susceptibility there is the question of conferred immunity. This appears usually in cases where one virus negatives the effect of another when both are present in the same host.

The whole question of immunity is overshadowed by the knowledge that a virus may " mutate " freely, and so change easily in almost all its characters, including its powers of infectivity and the symptoms produced in a given host.

Naming of Viruses

These complications of the virus position have not been simplified by the difficulties of naming the various kinds and their strains. The method up-to-date has been to give the virus a name indicating its host and the more obvious symptom it produces. For example, the virus which causes yellowish-white or greenish transparent patches to appear on the leaves of potato has been called " potato mosaic." This method was satisfactory until it was found that not one but many viruses could each produce " mosaic " in the leaf of a potato. Furthermore, the potato viruses are not confined to potato or even to its relatives in the genus *Solanum*. They infect other and quite unrelated hosts, and produce in them symptoms other than mosaic. Classifying viruses by the symptoms they produce or the hosts they infect is not satisfactory. Classification on the basis of their usual vectors breaks down too. The aphid *Myzus persicae* alone transmits at least twenty-six different viruses.

A recommendation made to the International Botanical Conference at Amsterdam in 1935 suggested a nomenclature based

on the name of the host followed by the word virus, then a number. Strains of the virus would then be indicated by a letter ; thus, cucumber virus 1B. The sub-strains of this are then indicated by a small letter, *e.g.* "a." This semi-official recommendation has not yet been adopted generally, and in practice the original method of naming by reference to the most usual host and the most usual symptoms still holds.

BOOKS FOR FURTHER READING

BAWDEN, F. C. *Plant Viruses and Virus Diseases* (Chronica Botanica Company, Waltham, Mass., 1945)

SMITH, K. M. *Virus Diseases of Farm and Garden Crops* (Littlebury & Co., The Worcester Press, Worcester)

Chapter XXV

MYCOLOGY

Having considered pathological conditions set up by factors of the environment and by viruses, the next study is disease caused by definite plant organisms. These are all lowly forms of life. In organization they may be simple, but in many of them the details of their life-history are complex. They show an extraordinary variety of forms, and differ very much in physiology. One characteristic they all have in common is that none contain chlorophyll. They may be green in colour, but the pigment is never capable of acting in photosynthesis. Apart from the chemosynthetic bacteria discussed on page 338, all fungi require a supply of true food.

It must not be thought that all fungi, bacteria, and the other classes of these lowly plant organisms are pathogenic (disease-causing). Many are saprophytes, and do a useful service in breaking down dead remains of plants and animals. Others are useful in that they " fix " gaseous nitrogen for other plants to use. Many are employed by man in commercial processes and form useful compounds for his use, as for example, yeasts in baking, brewing, etc. Finally, many, like the common mushroom, are edible and form a source of food. In agriculture, however, it is the pathogens attacking crops which attract the most attention. All the organisms involved are, as has been said, devoid of chlorophyll, and because they attack the living plant are classed as parasites. Some of these parasites, after having killed the host, live on the corpse and are then saprophytes. All differ from a virus in that they are visible at some stage of their life either to the unaided eye or under some degree of magnification.

Perhaps the simplest kinds structurally are the bacteria in which the individual is a single microscopic cell. The cell varies in shape from spherical to rod-like. It may be supplied with little threads of protoplasm which thrash about like whips and are called flagella. Each cell is simple as cells go, for it consists of a wall, protoplasm, and a nucleus so elementary in character as to be hardly worthy of the name.

Reproduction in these unicellular plants is of two kinds.

On the one hand, when conditions of food supply, temperature, etc., are suitable, each individual, by a process of simple fission, divides into two. This is quite devoid of any sexuality and is analagous to propagation in the higher plants. Division follows division quickly and multiplication is very rapid. On the other hand, when conditions become adverse, many forms of bacterium form a resistant structure. When this occurs, the protoplasm of the cell shrinks away from the thin cell-wall. On the surface of the shrunken protoplast a very hard wall develops. Inside this hard resistant coat the protoplasm is protected from extremes of heat, destructive chemicals, and other agents which would have destroyed the vegetative stage. The resistant stage is called the resting spore.

The bacteria are important in almost every aspect of agriculture ; in the soil, the dairy, the cheese room ; and as causes of disease in plants and animals.

The fungi are very varied in structural organization, but are always rather more complex than the bacteria. They may be arranged in classes.

The Slime Moulds

The slime moulds, or *Myxomycetes*, are a group with characters almost as much animal as plant, consisting as they do for a significant part of their life of a mass of multi-nucleate protoplasm.

Actinomycetes

The *Actinomycetes* are still very simple but nearer to the simple fungi. The plants consist of narrow, sparsely septate hyphæ. Spores are formed by the break-up of the protoplasm within the hyphal cells. The process of subdivision commences at the tip of a filament and spreads backwards. A number of them cause disease in plants and animals. Examples taken from these two groups will be described later on.

The True Fungi

A member of the true fungi always shows a definite structural organization. The unit of the vegetative body is the *hypha*, a long, thin, hair-like filament consisting of a wall lined with protoplasm. The hypha in some members is divided by cross walls, when it is said to be septate, or there may be no septa

present. The a-septate hypha has many nuclei and is said to be cœnocytic. In the septate forms the individual segments may contain one, two, or many nuclei. These latter types are also described as cœnocytic.

When many hyphæ go to make up one plant they are referred to collectively as the *mycelium.* The mycelium never shows any differentiation into root, stem, or leaf, but there may be regions showing some degree of specialization for function. Part of the mycelium may be purely vegetative, while another portion is specialized for spore production. This is clearly seen in the familiar mushroom, where there is a white mycelium ramifying through the soil, collecting food and water. Above ground there appears the umbrella-like, spore-producing organ. The underground vegetative portion sometimes forms a white cord-like similitude of a root, this is called a rhizomorph. It is to be remembered that the whole of the mushroom plant, in common with all other fungi, is constructed of hyphæ, loose in one part and compacted for a special purpose in another. The compacted portion of these, when examined microscopically, simulates a cellular tissue and is known as pseudo-parenchyma.

Propagation and Reproduction in the Fungi

The increase and spread of these plants is accomplished by means of the vegetative mycelium, asexual spores and sexual spores. The mycelium, when broken up, functions as a propagant just as parts of the body may do in higher plants. This is taken advantage of in mushroom growing, when a mass of mycelium in a suitable medium (called " spawn ") is used to propagate the crop. Asexual spores may be looked upon simply as small portions budded off from the mycelium and are therefore another but more specialized method of vegetative propagation. The sexual spores may be regarded as the fungal parallel of the seeds of higher plants, in which case the vegetative mycelium and its non-sexual spores may be regarded as the functional parallels of rhizomes and corms in propagation.

The disease-causing fungi, being parasites, are always faced with difficulty in completing their life-cycle, for in order to do so a suitable host must be found. Reproductive units must be very freely produced in order to ensure that some at least are successful.

The spore, which is the unit in reproduction, is almost invariably one-celled, not commonly two-celled, and is produced in enormous numbers. Different kinds of spores may be produced at different points in the life-cycle, but the total number is always very, very high.

Kinds of Fungal Spore

There are, as we have seen, two general classes of fungal spore. There are those which form by mere budding off from a hyphal tip and are vegetative spores. These are typically thin-walled and not resistant to adverse conditions. They are used for the rapid multiplication of the plant during periods favourable to the vegetative phase. These may be called summer spores, asexual spores, etc. On the other hand, there are the spores produced as a sequel to or as the result of a sexual act or fusion of gametes. The sexual mechanism in the fungi is often obscure and complicated, and in many cases is not well understood. Spores produced sexually are often capable of remaining dormant for long periods of time, or resisting conditions adverse to the vegetative state. These may be called sexual, resting, or resistant spores.

The terminology used to describe fungal spores is somewhat extensive, and only a few of those more generally applicable need be mentioned. The terms often refer to the method of their production, to a feature of their structure and appearance, or to the nature of the " fruiting " body in which they are produced.

When the spores are simply budded off from the tips of hyphæ they are called *conidia* or conidial spores. A few of the special names attached to special forms of conidia will be mentioned as they occur on the fungi to be described later.

Among the sexually produced spores, two broad classes may be remembered. Those produced by isogamy (fusion of morphologically identical gametes) are zygospores ; those produced by heterogamy (fusion of dissimilar gametes) are referred to as oospores.

Sometimes a special hypha or a group of special hyphæ is formed, in which a sexual act takes place. From each hyphal end four little filaments are produced. Each bears a small spore or sporidium like a bust on a pedestal. The hyphal end is called a basidium and the sporidia produced are called basidio-spores. When the basidia are massed in a special layer this is called a hymenium. Another fructification is the ascocarp, which has a

PLATE 101 VIRUS DISEASE

" Streak " in Tomato leaf and fruits

Cabbage ring spot

(Photos : Plant Pathology Service Dept. of Agric., Scotland)

PLATE 102 VIRUS DISEASE

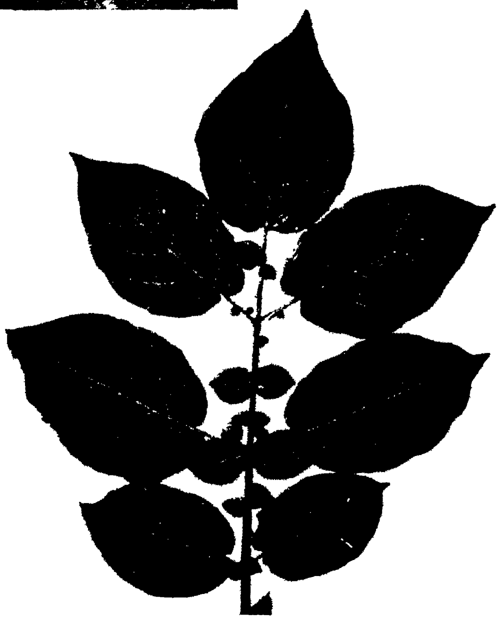
Leaf-roll in Potato (var. British Queen)

Aucuba disease in Tomato

(Photos : Plant Pathology Service Dept. of Agric., Scotland)

PLATE 103 VIRUS DISEASE

Severe mosaic in Potato



Mild mosaic in Potato

(*Photos : Plant Pathology Service, Dept. of Agric., Scotland*)

PLATE 104 VIRUS DISEASE

Top necrosis in Potato

Spotted wilt in Tomato

(Photos : Plant Pathology Service, Dept. of Agric., Scotland)

layer of sexually formed flask-shaped cells, each called an ascus (plural, asci). Each ascus contains up to eight peculiar spores, the ascospores.

The important points in connection with the increase and spread of disease-causing fungi are that reproduction is predominantly by spores; that they are produced in enormous numbers; and that they must reach a suitable host if they are to function.

Some fungi are strict in their requirements as to the kind of host they can infect; that is, they are specific to one host. Others can infect a wide range of host plants; they are non-specific. A few, such as some rusts to be described later, must infect two hosts alternately, passing by special spores from one to the other in each complete life-cycle. These last are said to be heterœcious.

Control of Fungi

Protection of the crop plant against disease follows two main principles, prevention and cure. The whole study of protection will be dealt with here, first generally, and then later with details illustrated by reference to individual diseases and their causative organisms.

Immunity to Fungal Parasites

Probably no method of protecting a crop against fungal disease is so attractive as the production and growth of an immune variety of host. If a variety completely immune to all diseases could be evolved in each crop, the practice of agriculture would be considerably simplified. This is hardly possible, but varieties showing heritable resistance to a specific disease are not only possible but are now well known. "Conferred immunity" acquired by a plant and lasting for the life of that generation only is also known.

When considering an immunity of a crop plant to a disease three main points must be kept in mind. In the first place, immunity to one disease does not confer immunity to another. Resistance to each of the diseases to which the plant is heir must each be bred for or developed separately. Hence, in writing of an immune variety, what is referred to is a variety which will not readily contract some specified complaint.

Secondly, complete and total immunity to a single disease in

an otherwise susceptible crop probably does not exist. A rather more accurate view is that some individuals or varieties are more resistant or less susceptible to a particular disease than are others. If, however, the pressure of infection on these resistant forms is increased past a critical point, or if environmental conditions are highly favourable to the parasite or adverse to the host, then the fungus may gain the upper hand.

Thirdly, the fact that in disease there are two components, the host and the parasite, must never be lost sight of. Just as resistant forms of the host may develop due to genetical alterations in it, so too changes of a heritable character may take place in the parasite which render it more virulent and capable of breaking down a previously existing immunity.

Many disease organisms have developed a number of strains or biological races, each showing different degrees of virulence but all morphologically alike. So a particular crop plant variety may be immune to one strain of a fungus but be quite susceptible to another strain. Very often the strains of different virulence, or different ability to attack, inhabit different districts or countries. Thus a crop plant variety immune to a definite disease in one geographical area may become infected by that disease when transferred to another area. So, too, the inadvertent transportation of a strain of fungus from its " home " territory to a new area may cause disease of the crops long resident there and immune to the local form of the pathogen. A case of this was seen when the wheat variety " Bobs " was taken from Australia to India and South Africa. Bred in Australia, " Bobs " had proved to be immune to the black rust there. In India and South Africa the immunity broke down completely. Either the black rust fungus of India and South Africa is of a different biological race from that of Australia, or growth in the new environment had so altered the wheat that the resistance mechanism failed.

Characteristics determining Immunity

In practically every case recognition of the special feature of the host which confers immunity depends on determining the point in the life-cycle of the host at which the fungus makes its attack, and the method by which a successful infection is then carried out. The matter is important, and its further study here will be profitable. At this stage of the discussion the unit by which the

fungus passes from a diseased plant to a healthy one may be assumed to be some kind of spore. The spore must reach that part or organ of the host through which, or on which, infection is possible, and it must do this at a time when the part is in a susceptible state. Should the host not be in an appropriate stage of development when the spore arrives, then seeming resistance occurs.

Take a simple case. If a fungus attacks through an open flower, a variety of a susceptible host which blooms either earlier or later than normal will be in the non-flowering condition when disease spores are available. Thus, this variety will escape or evade infection.

Again, though the fungus may produce its spores over a quite extended period of time, if a host variety by reason of earliness or lateness is in the susceptible stage only when weather conditions in most years are not suited to spore dispersal or spore germination, it will appear to be immune in those years when the weather does not suit the fungus, and show its susceptibility in other years.

These and similar cases of evasion of infection, while of considerable practical value, are not instances of true immunity. The degree of true resistance or of susceptibility possessed by any variety can only be assessed if the plants are exposed to viable spores when infection is possible and conditions are suitable.

External and Internal Parasites

Two broad classes of pathogen must be recognized. First, there are those where the fungal spore after germination on the surface of the plant produces a mycelium which, if the host is susceptible, enters the tissues and lives there. Secondly, there are those in which the adult mycelium remains on the outside of the susceptible plant, and draws its nourishment through hyphæ (haustoria) sunk down into the host tissues. Recognition of these two classes will be important later when discussing cure of disease.

Contact between Host and Parasite

Whether the parasite is an external one or one living in the tissues the infecting spore must reach, and remain on, the host until it has germinated and the first hypha has been produced. Should the surface of the plant be of such a nature that the spore falls

off, blows away, or is washed to the ground by rain, a degree of immunity will result.

If the surface of the plant does not provide a good " seed bed " for the spores they will not germinate successfully. For example, some varieties of potato have open, hairy haulms. These do not wet easily, and when wetted dry quickly. Hence, spores of the blight fungus which require moist conditions for successful germination and development do not succeed easily. In any but abnormally wet years such a variety will not be infected. So, too, in other plants possession of a very smooth, not easily wetted cuticle gives a similar sort of result with other fungi.

Given that the spores remain on the plant and germinate, the entry of the hyphæ into the tissues is the next point where immunity may depend on the conditions.

Entrance through a Wound

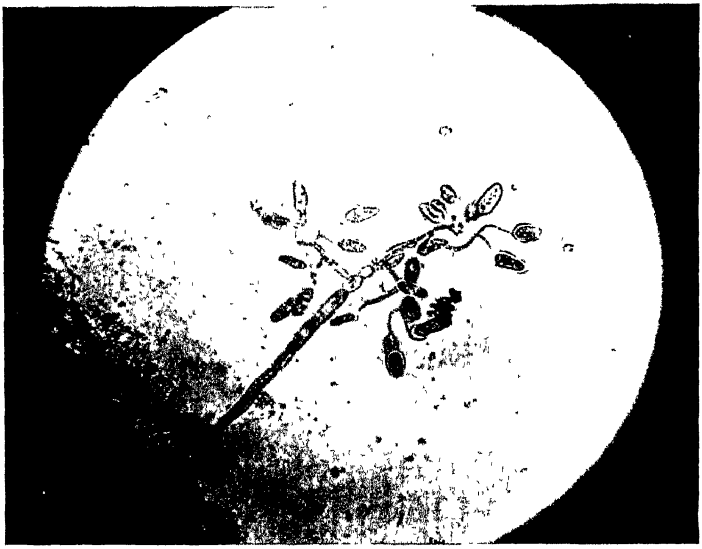
Wounds produced either accidentally or in such operations as pruning or mowing may provide a portal for some fungi. Many fungi do gain entry only through a wound, but many can enter the intact plant.

Entrance through the Cuticle

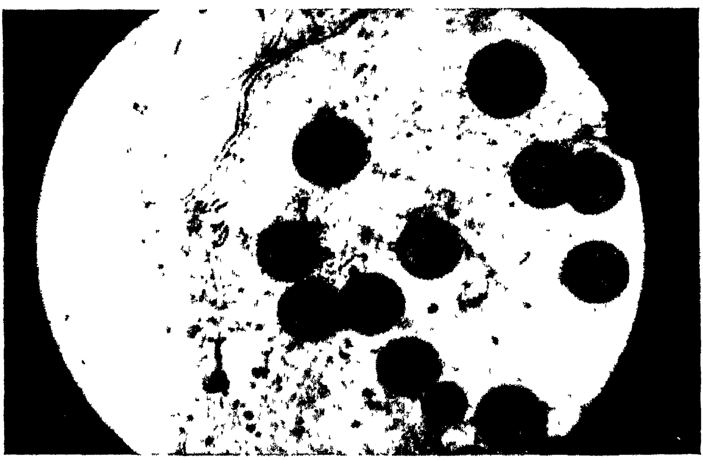
If the hyphæ do gain entry through the cuticle then some pressure or force must be exerted to push it through. No enzyme or other agent capable of dissolving cuticle is known in the fungi. The force developed by the hypha must be strong enough to force the tip through the surface covering. If the cuticle is sufficiently thick it may be able to resist penetration and so prevent entry of the parasite. This is the reason why on an infected plant it is common for older leaves and stems to show a lower degree of infection than young leaves not long emerged from the bud. Where the cuticle is thick a degree of immunity may arise.

Entrance through a Stoma-pore

Other fungi penetrate the tissues, not through the cuticle or a wound, but by way of the stoma-pore. In these cases the spore germinates on the leaf surface, and the hypha grows towards the pore. The filament passes through, and so into the tissues. It is probable that chance alone does not decide whether the advancing hyphal tip reaches a pore or not. There is evidence suggesting that the growing filament is definitely directed or attracted towards

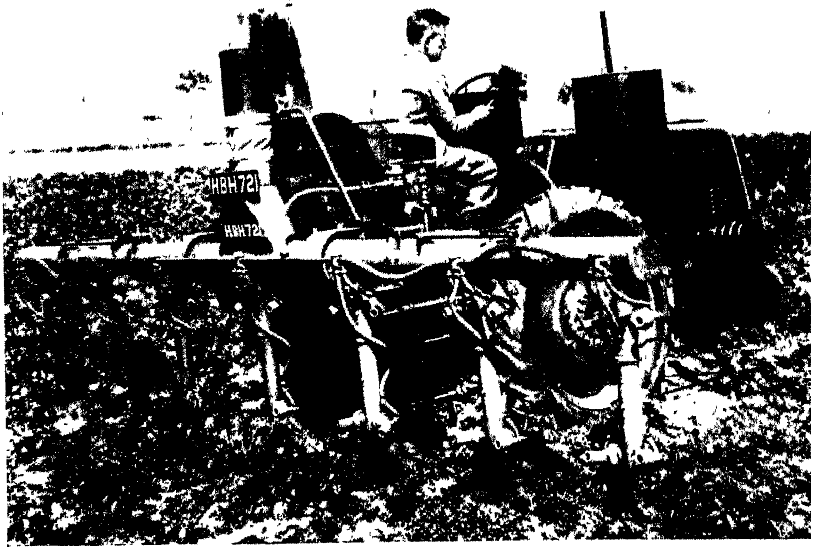


Thin-walled conidial spores



Thick-walled resistant resting spores
The spores produced by fungi usually fall into one or other of these two types

(Photos : Plant Pathology Service, Dept. of Agric., Scotland)



A modern machine for spraying crops

A mobile seed dresser. This machine is easily towed from farm to farm, where th home-grown seed grain is rapidly graded and dressed with fungicidal dust

(Photos : Plant Protection Ltd.)

the stoma. Some emanation, gaseous in character, issuing through the pore may cause the hypha to develop more in that direction. If this emanation is a gas normally present, say water vapour or oxygen during the day, or carbon dioxide during night, there is no chance of immunity arising. The movement of these gases is essential in the life of the plant and cannot be interfered with. On the other hand, if the emanation is of a special nature, say that of a volatile oil produced in the tissues of the plant, then any plant lacking the ability to produce the particular compound will show a lower degree of infection. Still more so, plants producing a volatile compound adverse to the fungus will be less easily infected. In either of these two cases selection and breeding may develop a resistant variety.

Immunity after Contact

Even if the process of infection goes so far that the fungal hyphæ succeed in entering the tissues of the host, immunity is still possible. The cells of the host, by reason of an idiosyncracy of hydrogen ion concentration or osmotic concentration of sap, may inhibit further development of the pathogen. Compounds such as tannins or glucosides, when present in the cells, may have a protective influence. In short, the fungus though in the tissues cannot grow.

A bar to the parasite occurs when the tissues, stimulated by the presence of the fungus, place in the path of its advance a layer of cork or a " plug " of gum. These form a barrier against the parasite and the attack is sealed off.

Finally, if the host is extremely sensitive to attack, the tissue at the point of infection may die very quickly. The dead cells do not provide a suitable substrate for the fungus, and it dies. Such hypersensitivity by localizing and starving the fungus may confer immunity.

Discovery and Selection of Immune Individuals

As will be seen in a following chapter, such characters of the plant as those which confer immunity to disease may be produced by a heritable (genetical) factor passed from one generation to the next in an orderly way. Such a genetical factor may arise quite fortuitously in individual plants and for no apparent reason. When, therefore, a few healthy individuals are seen in an otherwise

badly diseased crop, they should be marked; they may become the forerunners of an immune variety. Care must be exercised in this regard, for the freedom from disease of these first plants may be due to pure luck in that they were not supplied with spores. This point must first be settled.

Testing Disease-free Selections for True Resistance

The selected plants and their progeny must be grown in such a way that they are exposed to a truly significant degree of infection at appropriate times. If the progeny continue healthy or show a regular proportion of healthy to diseased individuals, selection and possible breeding work may continue.

Immunity introduced from Non-cultivated Relatives

In a number of crops no form immune to specific diseases is available, but closely related, highly resistant wild forms are known. For example, the cultivated potato is not immune to attacks of blight, but a South American relative, *Solanum demissum*, is. The cultivated potato will cross with *S. demissum*. The nuclear divisions of the hybrids obtained from the cross are very aberrant, but fertile progeny can be obtained. It seems possible that the chromosomes of *S. demissum* which carry the factors for resistance may be introduced into the potato nuclear complex, and so the genes for cropping, quality, and resistance to blight will be associated in one plant. When this association of chromosomes of dissimilar origin is organized into a harmonious functioning nucleus, potato varieties immune to blight will become available.

Vegetative Propagation aids Immunity

When a cultigen is increased by propagation, the production of sufficient stock "seed" for commercial introduction is simplified. Sexual reproduction with its probabilities of variation and a long breeding programme is eliminated.

Grafting and budding, too, provide opportunity for exploiting inherited immunity. For example, with fruit trees a "scion" resistant to a shoot disease may be grafted on to an otherwise non-resistant tree. Again, a wild "unimproved" but resistant "stock" may be used to provide the root system for a good variety susceptible to a root parasite.

There is evidence that between some stocks and scions more obscure relationships affecting immunity exist, for some stocks confer an immunity on some scions owing to an idiosyncrasy of their mutual physiology.

Conferred Resistance-Susceptibility

As distinct from these various heritable or genetical immunities, a degree of resistance, or extra-susceptibility to disease, may appear and continue during the life of one generation only. These cases are usually associated with some abnormality of the environment or the nutrition of the host. For example, it is well known that over-supply of nitrogen, expecially if accompanied by a copious supply of water, will produce a soft, sappy plant more easily infected than a less extravagantly nourished individual. It must not be assumed, however, that the converse is true, and that a poorly developed plant growing on a barren soil will be disease-free. In contrast to the effect of nitrogen, generous supplies of potash have a tonic effect on most crops, so that even if infection does take place, the disease is limited in its development.

Climatic factors, particularly humidity and temperature, may aid the fungus without assisting the host. Muggy, humid weather usually increases disease. This is well seen when blight of potatoes " flares up " in the crop during such a spell in late summer or autumn. Early potatoes often escape blight simply because they are harvested before the weather suitable to the fungus comes round. A somewhat similar case is seen in the relationship of wheat to " foot-rot." Winter wheat, if sown early, experiences a comparatively high soil temperature in the seed bed. The soil is colder when later sowings are made. Higher soil temperatures favour the foot-rot fungus, and infection of the early sowings is greater. Crops from late sowings show some degree of freedom from this disease.

Protection of Non-Immune Plants

When immune varieties are not available and evasion of disease not possible, the crops must be protected by more positive means. Sanitation in its broad sense is probably the weapon of greatest power available to the grower. So far as is possible, " reservoirs " from which infection can come should be eliminated from the farm.

Elimination of Sources of Infection

Weed-hosts and ground-keepers should be eradicated. These may enter into disease causation in one of two ways. On the one hand, when they are infected by the pathogen equally with, and in the same way as, the crop plant, they serve to carry a specific disease over parts of a rotation when the crop-plant host is absent. On the other hand, there are plants which, though unrelated to the crop, provide an alternative host for a heterœcious fungus, and when present allow it to complete its life-cycle. This is well seen in the rust fungi. A common rust of wheat infects barberry in late summer, and in the following spring the stage on barberry infects wheat. Elimination of the alternate host of such heterœcious fungi breaks the life-cycle of the fungus and tends to reduce the intensity of disease in the crop.

The Soil as a Source of Infection

The soil can carry over infection. Under certain circumstances, such as in glass-houses, soil sterilization by chemicals or steam may eliminate the soil-borne stages of fungi. In the field during the course of a bare fallow, intense sunlight, if it occurs, may have a sterilizing effect. Soil ameliorants such as lime, by improving the texture of the soil, altering the hydrogen ion concentration, may aid the plant and/or depress a soil-borne fungus. This is seen in "finger-and-toe" disease of turnips and other Brassicas. The spent lime from old-fashioned coal-gas purification installations proved to be an excellent soil fungicide, probably because it contained sulphur compounds of fungicidal character.

A rotation of crops which allows time for the disease organism in the soil to die before a suitable host reappears is often successful.

Spread of disease from an infected field to clean ground often takes place through dung. This is so in the case of "finger-and-toe." Though the spores of the pathogen are rendered harmless by passing through the intestines of an animal, the manure may be infective. If a diseased crop is fed to the animals, parts carrying spores may fall directly on to the litter and later pass out to the fields still fully infective. Great care should therefore be taken when crops infected with finger-and-toe and other plant diseases are fed in the uncooked state.

On the haulm

Two tubers, the left slightly attacked; the right badly diseased

The same two tubers cut in half

(Photos: Plant Pathology Service, Dept. of Agric., Scotland. Crown copyright reserved)

Common scab on Potato

Powdery scab on Potato
(*Photo : Crown copyright*)

Wart disease on Potato

Finger-and-toe on Swede Turnip

(*Photos : Plant Pathology Service, Dept. of Agric., Scotland*)

Seed-borne Disease

A crop sown on clean land may later show disease developed from spores carried in with the seed. Spores or mycelium may be in or on impurities such as pieces of earth, straw, chaff, etc. These should be cleaned out before sowing.

Efficient seed-cleaning and grading can help in another way. It happens in the case of some diseases such as stripe of barley that infected grains are small and stunted. By separating out the large plump grains and sowing only these, disease in the subsequent crop may be considerably reduced.

Prevention of Disease by Seed Treatment

When the seed is infected, and no method of separating out the healthy individuals is available, more positive measures using sterilizing agents must be adopted before the seed is sown. Choice of the agent to be employed depends on whether the fungus is borne on the surface of the seed or has invaded the deeper tissues.

Chemical substances, whether in the form of a dust, a liquid, or a gas, are usually most appropriate for use against surface-borne fungi, whereas heat, at a degree tolerated by the seed but fatal to the pathogen, is usually most effective in the case of an internal parasite.

Chemical Seed Dressings

Of the chemical agents commonly used two classes may be recognized: those which are temporary, and those which are persistent. The members of the temporary class, after application, disappear, probably by evaporation, during subsequent storage. The persistent forms remain adherent to the seed and are sown with it. By their persistency members of this latter class perform two functions. They may kill the fungus on the dry seed and then remain to kill any pathogen which may be in the soil to attack the young, vulnerable seedling.

Liquid Seed Dressings

At one time liquid fungicides—solutions of compounds of copper or mercury, formaldehyde, etc.—were used extensively against pathogens borne on the surface of seeds. These are not now so popular, as the procedure is messy, and cumbersome vats or

apparatus may be required. Another disadvantage is that the seed once treated with liquid does not store well, and has to be sown promptly after removal from the fluid.

When a liquid fungicide is used the seed, contained in a bag or other suitable container, is immersed in a vat of the chosen solution till every grain is thoroughly wetted. Thereafter, the bags are withdrawn and allowed to drain. When the grain is sufficiently dry it is sown.

An alternative method is to pile the loose seed in a heap and pour the fluid over it. Constant turning and mixing of the pile is necessary to ensure that each grain receives its quota of fungicide.

Dry Seed Dressings

Chemical compounds in dust form are now much more popular as seed dressings. All that is required is that the seed shall be mixed with sufficient of the dust to ensure that each grain is lightly coated with the material. Large lots are mixed in a mechanical bulker. Smaller lots may be conveniently treated in so simple a piece of apparatus as a discarded end-over-end barrel churn. Even simpler methods may be adopted on the farm. Many of the dusts when inhaled are noxious to human beings, and precautions for the safety of the workers have to be adopted. The treated grain if eaten may poison farm animals, and care should be taken during storage. The greatest convenience attaching to the use of dusts follows from the fact that after treatment the seed may be stored for an indefinite period.

Seedsmen possessing suitable machinery can conveniently dust large bulks of seed and then distribute the treated grain, as required, to their customers. The cost of this large-scale dusting is not great, and a very small addition to the price charged for the seed recompenses the seedsman for the service. It is to be noted that dusts are persistent, and serve to protect the seedling not only from seed-borne fungi but from many disease organisms already in the soil.

Control of Disease carried Inside the Seed

Attack on a fungus lying deep in the tissues of the seed is much more difficult. Chemicals do not readily penetrate to the seat of the trouble, and those which do may easily injure the embryo,

causing loss of germinating power. Moist heat seems to be the only agent which, in careful hands at least, causes no harm to the seed.

Essentially the procedure is to soften the grain for some four hours in cool water at about 20° to 30° C., and then to raise the temperature to about 50° C. The actual temperature used depends on the kind of seed and fungus, but in every case it must be very carefully controlled, for if just a little too low it will fail to kill the fungus, and if a degree or so too high it will kill the seed. The margin of error either way is small. The temperatures used in the control of loose smut of wheat or barley are given on page 499. After treatment the seed is drained, dried, and promptly sown.

Obviously the method, in being messy and requiring cumbersome equipment, shares in all the disabilities attaching to the use of liquid fungicides.

Control of Disease in the Growing Crop

In dealing with disease in relation to a growing crop, active measures of control usually partake of prevention in part and attack in part. The agents used may be in the gaseous, liquid, solid, or colloidal state. Examples include aqueous solutions of metallic compounds such as those of copper; a solid-in-liquid colloidal dispersion of an element like sulphur; or solids such as flowers of sulphur applied as dusts. Hydrocyanic acid gas (prussic acid) is sometimes used where the plants occupy a confined space. Sulphur may be burned to fumigate a glasshouse.

Liquid-in-air colloidal dispersions known as aerosols are also used. These last are important, as they permit of a wider choice of substances as fungicides. The fungicide of choice, though not soluble in water, may be dissolved in a small quantity of another liquid. The solution is then dispersed in water and the mixture blown into a mist or aerosol.

The many mixtures and methods in use to-day are all designed to bring the fungicidal material and the fungus into as intimate contact as possible. If the material is then retained on the surface of the host it prevents a renewal of the infection. In order to achieve intimate contact, the fluids used must be of as low surface tension as possible so that " wetting " is complete.

"Wetting agents" are often included in spray mixtures. Fluids should be applied to the crop as a fine mist so as to penetrate to, and wet, all its parts. The use of gas where applicable gives the finest penetration and contact.

Having achieved the best possible contact between the fungicide and all parts of the diseased plant, it is then important that the active substance should remain *in situ* to prevent further development of the disease. In some cases evaporation of the solvent leaves a non-volatile fungicide deposited on the plant. This is not always satisfactory, for if the chemical is soluble in water, rain later may wash it away. The effect of the fungicide is more lasting if it is composed of particles which are adsorbed, either by capillary forces, or by virtue of the surface and the fungicide possessing electrical charges of opposite sign. Aerosols are particularly effective in this regard.

Almost all these measures apply to fungi borne on the surface of the host. When the pathogen inhabits the inner tissues it is almost impossible to get at it with a curative agent, though cases are known where inorganic salts, applied like a manure, enter the plant and effect a cure.

In a crop, where practicable, individuals affected by an internal fungal parasite should be pulled out and destroyed. The infected parts of a fruit tree may be cut off. These measures serve to arrest the development of an attack.

Many of the diseases of agricultural crops do not kill the plants but merely reduce their efficiency. In these cases the grower tolerates the reduction of yield but takes appropriate steps against a similar attack in the future.

It will be seen from what has been said that in dealing with any particular disease a great deal of information is required about it. It is necessary to know what hosts are affected; how and when spores are released; the method by which infection takes place; what, how, and when curative measures should be tried. The procedure is first to identify the disease precisely, then consult the literature already available. Ability to recognize particular fungi is best acquired by seeing as many kinds as often as possible at all stages of their life-history.

In a general account such as this no more than examples of different types can be provided. Those given here have been selected to exemplify significant biological points and to illustrate the application of the principles already outlined.

Bacteria

These very lowly plants are extremely minute, and under favourable conditions reproduce extremely quickly by fission. Some form spores, but none of those causing disease in plants do so. The systematic naming of the bacteria has not yet been stabilized, and here the descriptive name of the disease will be used to designate the causative organism.

Black-leg of Potato

Black-leg of potatoes is of widespread occurrence, and is quite a good example of a bacterial disease of plants. The lower parts of the haulm of an infected plant are seen to blacken and rot; the leaves turn yellow and curl. The organism is found in the plant inhabiting the intercellular spaces of parenchymatous tissue. When present in the tubers it causes rotting, usually at the heel end. In a mild infection no symptom may be observed externally on the tubers, but when one of them is cut in halves the cut surface readily blackens on exposure to air. If infected tubers are used for " seed," the resulting plants will be diseased. Indeed, the shoots which arise from a diseased " seed " may die early and the crop fail. The disease organism can lurk in the soil and from there infect the tubers through the cuticle. Early varieties seem to be more easily attacked than later varieties. In clamps or pits the disease spreads rapidly unless ventilation of the heap is fully efficient. It is believed that when insects in the soil or clamp bore holes in a tuber, infection by bacteria follows. In the United States of America the " seed-corn maggot " is thought to carry disease-causing bacteria into the wounds it makes.

Actinomycetes

This group shows relationships with both the bacteria and the true fungi.

Common Scab of Potatoes

Common potato-scab is caused by a member of the Actinomycetes group. " Scab " should perhaps be written in the plural, as there are probably more than one kind and more than one strain of closely related organisms involved in their production.

Infection of the tuber takes place through the lenticels, and also through the skin in their vicinity. As a result small brown spots appear superficially. These spots extend, and where they occur the skin of the tuber ruptures. The rupture follows after the formation of a cork cambium in front of the invading pathogen. The tissues external to the cork layer lift and partially disintegrate, and the scab takes on its typical appearance. The individual scabs may be so large or so near enough to each other that they coalesce. When this happens the whole surface of the tuber may become completely covered by the rough, brownish lesions.

Scabbed tubers are not attractive in appearance, though their edibility when peeled is unimpaired. Many people think that scabbed potatoes are drier and of better eating quality than the healthy tubers.

The disease is more prevalent on well-aerated soils (gravels and sands), and is often found where town manure containing much coal ashes has been added to the soil in quantity. The hydrogen ion concentration of the soil, too, is a factor in the development of the disease. Alkaline soils favour attack. Green manures when incorporated in a soil seem to attract the organism, so that the potato tubers are " ignored."

The scab affecting mangolds and beet is closely related to scab of potato, though the two organisms concerned cannot interchange hosts.

Myxomycetes

These " slime fungi " are related to the lower fungi, though at one time they were regarded as a form of animal life.

Finger-and-Toe Disease

The organism causing finger-and-toe disease in crucifers is a member of this group. The plant itself is a naked mass of slimy protoplasm called a *plasmodium*. The plasmodium flows or streams, and so moves from place to place.

When conditions become adverse the plasmodium (which is multi-nucleate) breaks up into a large number of uni-nucleate portions or spores, and these may rest in the soil for many years. When one of these resting spores is moistened, as in a well-watered soil, the spore germinates and forms a small protoplasmic

(amœboid) body possessed of a cilium or whip-like organ. By the lashing of this cilium the amœboid body moves about in the soil water. When an individual at this motile stage comes in contact with the root of a turnip or other crucifer, it enters one of the superficial cells. Thereafter, by fusion with other similar bodies or by its own growth, it soon fills the cell of the host plant with a plasmodium.

The presence of plasmodia in the root cells causes them to enlarge and the host tissue to proliferate, so that galls form. The presence in the tissue of the gall of giant cells full of the naked mass of protoplasm differentiates finger-and-toe from all other gall-forming diseases in crucifers.

In course of time each plasmodium breaks up into many spores, which fill the host cell cavity. When the gall breaks up or disintegrates the spores are set free in the soil ready to initiate another life-cycle.

The disease is often counteracted by sufficiently heavy dressings of lime. Drainage, too, is helpful. Extension of the rotation so as to omit a cruciferous crop, especially if accompanied by complete suppression of cruciferous weeds, is helpful. Some varieties of swede, the seed of which is in commercial supply, appear to have a degree of resistance to the disease.

"Powdery" or "corky-scab" of potatoes is caused by a similar organism, but is usually most prevalent on soils of higher water content and at lower temperatures. Some forms of potato scab are very similar in appearance to wart disease of potatoes.

The True Fungi

The fungi are very varied in structure, life-history, and physiology, hence more than one example will be required to illustrate the group adequately. The method will be to describe first those simplest in morphology (though perhaps not simplest in life-history), and then proceed to more advanced forms.

Wart Disease of Potatoes

"Wart" disease of potatoes occurs in potato crops widely distributed over the world. Very few of the important potato-growing regions are quite free. Since two wild relatives of the potato, nightshade and henbane, have been artificially infected with the disease, and tomato crops have contracted it in disease-carrying

soil, the danger of plants other than potato acting as hosts cannot be ignored. The disease is most readily recognized from the "warts," which form on infected potato tubers but not on the true roots. Warts which do occur on potato roots are due to another fungus. The life of the plant in general is not affected by the presence of the growths.

Infection of the host is caused by small, motile, naked protoplasmic bodies resembling lowly animals, and therefore called zoospores. These when present in the soil water enter the young tuber at or near an eye. They then get inside a cell of the host and there enlarge. Later, the mass so produced rounds off and forms a wall. Through a pore in this wall protoplasm is extruded to form a thin-walled sac, and inside this, thin-walled spore-bags (sporangia) develop. Each sporangium contains 200 to 300 nuclei, round each of which a zoospore organizes. The sac or collection of sporangia (a *sorus*) swells up, bursting itself and the host-plant cell inside which all this has taken place. The sporangia in this way are forced out into the soil and the zoospores are released. Each zoospore is motile and may go on to infect another potato eye. Alternatively, the zoospore may behave as a gamete and fuse with one of its fellows to form a zygote. This zygote is also motile, and has two whip-like flagella. The zygote, like the zoospore, infects a potato tuber. After the host cell has been penetrated by the zygote type of motile zoospore, thick-walled sporangia are produced. These serve to carry over the fungus in the soil.

Some potato varieties possess a high degree of immunity to the disease, a character which is inherited. It is to be noted that an immune variety grown on infected soil may "carry" the disease in adherent soil. Once the disease is in the soil there is no practical method for its eradication. In Britain stringent measures are enforced in order to control the spread of the disease.

An allied organism causes "crown-wart" in lucerne. This disease is most prevalent in any area when surface flooding of the soil occurs, as sometimes happens on irrigated land.

Damping-off Disease

"Damping-off" of seedlings is caused by a soil-borne fungus. When seedlings (cruciferous forms are particularly prone) are grown crowded together and over-watered, the disease usually

Celery seedlings showing typical lesion at soil level

Tomato seedling showing typical felled effect

(*Photos : Plant Pathology Service, Dept. of Agric., Scotland*)

Leaf of Potato showing typical lesions caused by blight

Stored Potato tuber showing dry rot caused by blight

(*Photos : Plant Pathology Service, Dept. of Agric., Scotland*)

appears. Single plants and then whole groups fall over, like trees felled at ground level. This is due to hyphæ, which develop from resting spores in the soil. These attack the seedling at ground level and kill the cells.

During the early stages of an attack the hyphæ do not actually enter the cells of the host, but remain in the intercellular spaces.

After the death of the seedling the fungus continues to grow on the dead body, so that it behaves first as a parasite and then as a saprophyte.

During the period while the host remains alive, the fungus produces myriads of thin-walled conidiospores for the immediate spread of the parasite.

On the death of the host the fungus develops sex organs. First a peculiar sac, a female organ called an *oogonium*, is formed. This contains a number of large non-motile gametes. Close to the oogonium a male organ, known as an *antheridium*, develops. The male gametes pass from the male organ through a connecting tube to fertilize the eggs in the oogonium.

Each fertilized egg forms a thick wall round itself, and becomes a resting spore. This thick-walled spore retains its power to germinate until conditions are again suitable for the fungus. The fungus under certain circumstances can produce zoospores instead of conidia.

In cases where the method is practicable, sterilization of the soil before sowing seed prevents the disease. Seed should not be sown thickly. Watering should be done with care, so that " free " water does not appear round the " necks " of the seedlings—that is, at soil level.

Blight of Potatoes

Potato blight is closely related to the damping-off fungus just described.

Blight is present when brownish-black patches appear on the upper surface of the potato leaf, and below each patch on the under surface of the leaf a white fuzzy or dusty appearance is seen. The white fuzz of dust consists of masses of conidiospores. These are blown about by the wind. In humid conditions the conidia germinate promptly, and in a potato crop during a spell of warm damp weather an epidemic may soon be under way.

Each conidiospore, if germinated at higher temperatures (about 24° C.), produces a germ-tube directly. At lower temperatures

(12° C.) it produces zoospores. Each zoospore on the potato leaf puts out a hypha or germ tube. The germ tubes either pass through the cuticle or go down a stoma pore and so enter the tissues, where each forms a mycelium. The tissues of the host adjacent to the mycelium die. The dead tissue forms the brown patches in the leaf already referred to. Zoospores washed into the soil by rain infect young tubers either through the cuticle, or through wounds, or through the eyes.

Conidiospores or zoospores adhering to the surface of the tubers when they are clamped (pitted) may also cause infection.

Mycelium inside a potato in a pit does not produce spores, and there is no transmission from the diseased to the healthy tuber at this stage.

An infected tuber is easily recognized, for after it has been in the clamp (pit) for a little while brown patches are seen under the skin. In dry storage this is a dry rot, but if the clamp is wet secondary organisms invade the dead, brown patches, and a wet-rot ensues.

In the field the rate of spread of the disease on the haulms depends on climatic conditions. Humid, sultry weather with light rain favours rapid spread from plant to plant and field to field.

The rate of spread downwards from haulms to tuber is conditioned by any factor which facilitates or impedes the passage of spores into the soil. Tubers which are deeply covered by drills which have been well "set-up" may escape infection almost entirely and therefore store well. Copious rain beating down on badly diseased haulms will carry spores deeply into the soil, especially if the ridges are flat-topped or shallow.

In well-aerated, open soil the tubers form a thicker cuticle, and this is believed to confer a degree of immunity. Some potato varieties in cultivation seem to have inherited a degree of immunity to the disease. Some relatively unimproved wild forms of potato are quite resistant to blight, and there is now good reason to hope that the plant breeder will soon produce a fully resistant form from hybrids between wild and cultivated types.

Complete control of the disease can be obtained by spraying the crop periodically with either Bordeaux or Burgundy mixture, both of which are active fungicides containing copper. The first application of the spray should be given early before symptoms of the disease appear, and repeated throughout the season.

The season when blight of potatoes is likely to occur varies in different districts, but it is always possible during humid, warm spells at any time after mid-summer.

How long the blight organism may persist in the soil probably varies with circumstances, but it is certain that if the humus content is high and due to potato haulms the period is quite a long one. The chief source of the annual infection of the crop comes from the planting of diseased tubers. Seed potatoes should be closely examined before planting, and any showing brown patches rejected. Ground-keepers, often plentiful round the sites of old clamps of previous years, are frequently a fruitful source of infection.

Pink Rot of Potatoes

A close relative of the blight fungus causes this disease, which is prevalent on potatoes only in wet districts where the soil is infected. The fungus lives in those tissues of the host situated below soil level. The first symptom of an attack of pink rot is the wilting of the haulm.

These two potato disease fungi or near relatives of them (*Phytophthora*) occur all over the world, and cause many serious diseases of rubber, citrus, coconut, and other crops.

Downy Mildew of the Hop

The organism which causes this disease occurs as a mycelium in the " root stocks " of wild and cultivated hops. This vegetative mycelium inhabits the parenchyma of the cortex, pith, and medullary rays.

In the spring the infected " crowns " produce stunted shoots or " spiked growths " which bear small, brittle leaves. The upper surface of the affected leaves appears silvery, while the under surface is blackish violet in colour. This dark coloration is due to the presence of a dense mass of conidia-bearing hyphæ (conidiophores).

In wet seasons the disease is quickly spread by conidia and the trouble soon becomes epidemic.

Control takes various forms. If the " spiked growths " produced in spring are promptly pulled off and burnt, lateral buds situated in the lower, non-infected parts of the plant develop and produce healthy shoots. If the number of infected plants in a

hop garden is small, all of them should be dug up intact and completely destroyed. Spraying a partially diseased crop with Bordeaux mixture provides a means of control, but in Britain this fungicide must not be used once the hop (the inflorescence) has developed. Wild hops growing in hedges and waste places should be dug out and destroyed, for they often provide centres for the reinfection of the crop.

Many other mildews are well known, such as those occurring on onions, beets, roses, peas, crucifers and other plants. Spraying a mildewed crop in some of these cases is successful in combating the fungus.

Hop Mould or Mildew

This disease is found on the leaves of growing hop plants and the young hops (inflorescences). On the outer surface of the host-plant there is a copious mycelium with haustoria penetrating down into the leaf tissues. The individual hyphæ are septate, and each section or cell contains one nucleus.

Rapid spread of the disease after an outbreak has commenced is by conidia, which are produced in large quantities all summer. In autumn a "fruiting body" is produced. This contains many asci. An ascus at first is a somewhat cylindrical or elliptical cell containing one nucleus. The nucleus, by a series of divisions, gives rise to eight daughter nuclei, each of which has the reduced or haploid chromosome number. Each of these eight nuclei forms a cell wall about itself and becomes an ascospore inside the ascosporangium or ascus. The asci occur in groups surrounded by sterile filaments. The whole makes a definite structure or *ascocarp*. The "fruiting body" or ascocarp in this fungus is a closed body with the asci inside. Such a structure is called a *perithecium*.

The production of asci and ascospores is typical of a large group of related fungi called the ascomycetes. The fruiting body in other members may not be a closed structure ; it may be an open cup, or *apothecium*.

The perithecia formed by hop mildew on the hop plants in autumn fall to the ground or remain on dead hop bines left lying about. In these positions they pass the winter. In spring the perithecia eject the ascospores into the air and these are then carried by the wind to infect the new growth of the hop plant. If sulphur is periodically dusted on the plants during the growing

Hops showing typical brown discoloration of the " petals " and spots on the leaf due to downy mildew

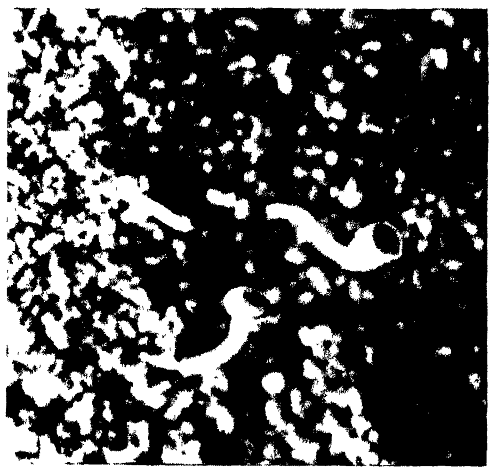
Hop plant showing a few normal bines and many short spike growths from the stool—a condition caused by downy mildew

(From E. S. Salmon and Wm. Ware, Leaflet " The Downy Mildew of Hop," S.E. Agric. Coll., Wye, Kent)

Leaf of Hop showing spots of mould

(*From E. S. Salmon, Leaflet "Hop Mould and its Control," S.E. Agric. Coll., Wye, Kent*)

Lesions in the stem of Artichoke caused by the same fungus (or a nearly related one) as causes clover rot



Apothecia growing out of a sclerotium in the soil

CLOVER ROT AND RELATED DISEASES
(Photos : Plant Pathology Service, Dept. of Agric., Scotland)

PLATE NGUS DISEASES—ERGOT

Left, The sclerotium germinated to produce stroma heads, each producing many spores which infect the grass flower. (*Centre*) The nfected grass (ryegrass) in the " honey-dew " stage. (*Right*) The grass head (rye) at harvest showing the sclerotia

(*Photos : Plant Pathology Service, Dept. of Agric., Scotland*)

season the mildew mycelium is inhibited. Varieties of hop showing a hereditable resistance to the fungus are known.

The true mildews (*Erysiphaceæ*), of which hop mould is a member, occur all over the world and on a wide variety of hosts. All are subject to control by sulphur. The element itself may be used as powder (flowers of sulphur), in colloidal dispersion, as a vapour, or as a chemical compound in solution. Intimate contact between the sulphur and the fungus is essential for the best fungicidal action.

Clover Rot and Related Diseases

The fungi so far considered have all been specific to one host plant or at least are restricted to closely related members of a group. It will be well now to mention a pathogen which is more catholic in its tastes. The fungus known to science as *Sclerotinia sclerotiorum* produces serious disease on such widely different crops as potatoes, carrots, lettuce, mangolds, tomatoes, beans, and a number of garden ornamental plants. The tips of the hyphæ of this fungus growing in the tissues of a host secrete a toxic substance which diffuses in front of the advancing mycelium, killing the host protoplasm and softening the cell walls. Luckily, the toxin cannot soften cuticle or cork, so with few exceptions the fungus can enter a host only through a wound. The exceptions are curious. If spores of the fungus alight on the stigma of the flowers of some plants, hyphæ are produced. These penetrate into the plant through the loose tissues of the style very much as a pollen tube would normally do.

The mycelium of this fungus forms a white mass in any cavity inside the host or on its surface. In these situations the hyphæ aggregate into a hard mass, irregularly roundish in form. This hard resistant mass of hyphæ is known as a *sclerotium.*

When the host dies and rots the sclerotia reach the soil. Here they lie quiescent for an indefinite time. When the sclerotium does germinate it throws up a number of cup-shaped apothecia, each borne on a long stalk. Each cup contains many asci, and each ascus contains a number of ascospores. Every sclerotium on germination provides a very large number of spores. The spores are discharged into the air. If any come to rest on a wound of a susceptible plant, infection follows.

In hot-houses steam sterilization of the soil "cooks" the sclerotia and gives some degree of control. In the field deep

ploughing, by burying the sclerotia, prevents germination or spore dispersal.

Clover rot, caused by this fungus, is only one of the forms of clover sickness. This particular disease is easily identified. When red or alsike clover plants die and rot during a humid, muggy autumn or in dull, warmish weather in spring, *Sclerotinia* may be suspected. The outer leaves of the rosette rot first, but later the whole plant becomes black and rotten. At first, individuals in the field succumb, but soon large patches of dead plants are seen, and finally all the plants in the field may be killed. The nature of the disease will be confirmed if close examination of the dead plants or the soil around them reveals the presence of sclerotia. These bodies measure some 5 mm. across.

The disease, if it is going to appear, nearly always does so in the first year of the clover ley. Second year and later crops are rarely if ever affected. Most kinds of clover except white may be attacked, and red clover is particularly susceptible.

After a clover crop has been lost in this way the land should be deeply ploughed in order to bury the sclerotia. No clover other than white should then be sown on the land for at least eight years.

Ergot

Ergot is another common fungus which forms sclerotia. It infects many grasses, but never clover. The ascospores of ergot infect the grass flower in spring and early summer, and the mycelium develops in the tissues of the ovary.

While the host is still succulent, hyphal endings come to the surface of the ovary where they bud-off conidia and secrete a sweet fluid. This is called the "honey-dew" stage. The sweet fluid attracts flies, which become smeared with it and with spores. When the flies pass to another grass flower they carry the mixture and so spread infection.

As the infected grass ripens, the mycelium increases to such an extent that it almost entirely replaces the ovary. The hyphæ then compact to form a hard sclerotium which completely replaces the grass caryopsis. The sclerotia may be harvested with such normal grains as are on the grass head or may be dropped on to the ground.

In spring, each sclerotium, sown with "dirty" seed or left on the ground from the previous year, germinates. It then

throws up numerous stalks, each bearing a round head called a *stroma*. In each stroma many perithecia are immersed. One perithecium contains many asci, each of which contains eight ascospores. The total number of spores produced by one sclerotium is very high. These ascospores infect the grass flower.

The interest in this fungus lies not in the slight harm it does to the host plant but in the effect it has on stock. The ergots contain a mixture of alkaloids which when consumed by a pregnant mammal cause rapid and powerful contraction of the uterus, so that premature birth ensues. The sclerotia and the alkaloids separated from it are used in veterinary and human medicine.

Consignments of cereal grains containing ergots, if not properly cleaned before milling, lead to serious disease amongst humans. A diet containing ground sclerotia causes gangrene of the limbs and other serious symptoms.

A sterol, ergosterol, which was first isolated from ergot sclerotia is the " mother substance " of Vitamin D, or calciferol. Irradiation of ergosterol by ultra-violet rays converts it into the vitamin.

Smut Fungi

These fungi commonly parasitize members of the grass family, and when they occur on a cereal grain such as wheat or oats are to be regarded seriously. The parasite lives deep in the tissues of its host, and there is not visible to the naked eye, nor is it subject to control. The mycelium grows in and along with the host axis, and so the active hyphæ are always at or just behind the growing point of the shoot. When the cereal forms flowers the fungus invades the ovary. Later, the ovary becomes filled with a mass of black fungal spores, which entirely replace the normal structure. It is from this that the smuts receive their name. They are readily recognized when the infected plant produces not grain but this mass of brownish-black, soot-like spores. These spores serve the fungus by infecting a new host, and the life-cycle is repeated.

From the point of view of control it is to be noted that in this group the parasite is vulnerable only when the host is in the " seed " stage, and therefore an attack on the fungus must be made by treatment of the seed.

Loose Smut

It is very important to recognize that there are two kinds of smut. There are, on the one hand, the "loose smuts," and on the other the "covered smuts." In the case of the loose smuts the spores produced in the ovary burst the "seed" coverings when ripe, and appear as a *loose powder*. This occurs when the normal, unaffected healthy plants are flowering. The spores are blown about on the wind. If one reaches and settles on the stigma of a suitable host, it germinates there and produces a hypha, which passes down to infect the young ovary. The resemblance between the behaviour of one of these spores and a pollen grain is striking. When the infected ovary dries-off as is usual at harvest, the mycelium inside becomes dormant and does not become active again until the grain rehydrates, when wetted prior to germination. In summary form it may be said that loose smuts produce their spores and set them free at flowering time. They infect the new host before its grain forms. *At harvest the fungus is inside the grain.*

Covered Smuts

In the case of the "covered smuts," the soot-like spore-mass remains enclosed inside the intact "seed" coverings. These envelopes filled with spores behave as a unit. These units are harvested with the crop and accompany the good grain to the stack or fall with it to the ground. Either in the soil or at thrashing the spore-mass breaks up and sets free the spores. The spores freed in the thrashing machine adhere to the surface of the good grains. The interest of the farmer is primarily directed to the spores on the surface of grain destined for seed purposes.

Germination of the "seed" and spore takes place practically simultaneously. The hyphæ developed from the spore invade the seedling. In covered smut, then, the tissues of the ripe "seed" are free of the fungus, and infection takes place in the seedling stage. *At harvest the fungus is outside the grain.*

One exception to these general statements regarding the cereal smuts must be noted. The spores of loose smut of oats, while they are blown about at harvest time, do not infect the flower but adhere to the grain and are harvested along with it. For practical purposes it behaves like a covered smut, and is subject to the same control methods.

PLATE 115 FUNGUS DISEASE—SMUT FUNGI OF CEREALS

Loose smut of Oats

Loose smut of Barley

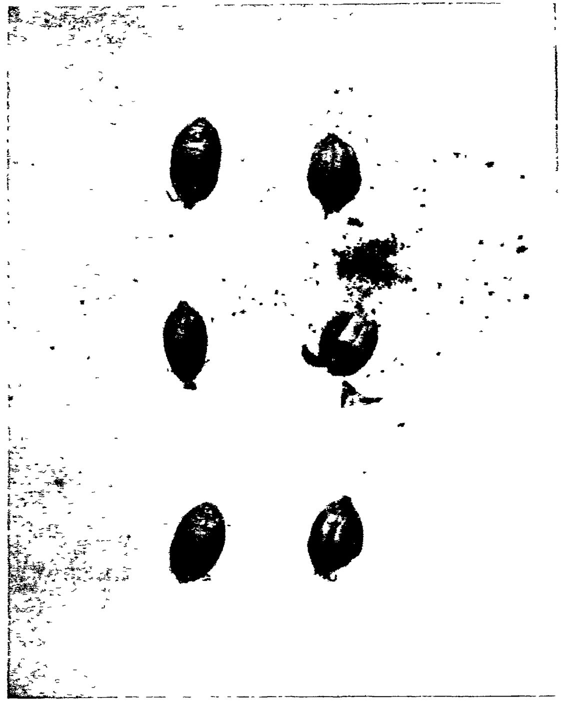
Covered smut of Oats

Covered smut of Barley

Loose smut of Wheat

(Photos : Plant Pathology Service, Dept. of Agric., Scotland)

PLATE 116 FUNGUS DISEASE—BUNT



(*Left*) Two heads of Wheat, one bunted the other healthy. (*Right*) Grains of Wheat affected by bunt ; one has burst, releasing the spores (*Photos : Plant Pathology Service, Dept. of Agric., Scotland*)

Control of Covered Smut

In combating the covered smuts (and loose smut of oats) any chemical is effective which either kills the spore or adheres to the seed and kills the hypha which come from the spore. Steeping the "seed" in a liquid fungicide is no longer a popular method. Dry dusts are now almost universally used.

Control of Loose Smut

Surface dressings, either liquid or dust, are not effective for the loose smuts, for here the mycelium is inside the grain. Heat treatment of the seed is the most effective control method. The grain is first soaked in cool or lukewarm water for about four hours. This preliminary soak brings the various structures into a condition that allows the heat to act. Next, heat is applied by transferring the "seed" to hot water. For loose smut of barley, steeping for five minutes in water at 49° C., followed by ten minutes at 51° C., is advocated. For loose smut of wheat the times in the hot water are the same, but the temperatures employed are a little higher, 52° C. and 54° C. Loose smut of rye is caused by the same fungus as loose smut of wheat and should be treated similarly.

Bunt

Bunt is often confused with smuts, and shares with them the old common name of "Brand." Bunt occurs on wheat, and to some extent on rice. Infected grains are shorter and more spherical in shape than normal. The groove which runs down the "face" of the grain is abnormally shallow. The colour of the caryopsis is grey or greyish-black. The bunt fungus spores remain inside the grain coverings at harvest. On crushing an infected kernel a fishy smell is at once obvious. This characteristic is referred to by another common name for this disease—"stinking smut."

Bunted grains are harvested with sound ones. The spores germinate when the healthy wheat "seed" germinates, and the seedling is infected. The mycelium grows along with the apical meristem. There is some evidence that if the wheat is induced to grow very quickly the fungus can be "left behind," and some measure of control is obtained. Control of bunt is the same as for the externally borne smuts.

A crop infected with these smuts or bunts should not be used as a source of seed, but the whole of the grain consumed. Varieties

are known in each of the different cereals which are resistant or immune to the smut or bunt fungi. Care has to be taken in accepting statements made in this regard, for there are many biological races in these fungi. Just as the grain varies in its physiological relationship (susceptibility-resistance), so does the fungus vary in ability to attack.

The Rust Fungi

The rust fungi rarely cause death of the host plant, but by their action they often reduce crop yields by a considerable amount. The rust mycelium ramifies in the shoot tissues of the host, and in some cases it may be generally distributed, while in others it may remain localized. Wherever the hyphæ invade, the tissues die. Many of the rust fungi produce spores which are reddish in colour, and this gives rise to the common name. There is a large number of different kinds of rust recognized by differences in spore structure and other morphological characters. Some are heterœcious ; in the life-history of others only one host is required.

Black Rust of Cereals

Black-rust or stem-rust of cereals may be taken as an example of the many forms which occur, each with its own specificity of host(s). All four of the common cereals (wheat, barley, oats, and rye) may become infected. Some wild grasses, particularly couch (*Agropyrum*), are also subject to attack.

In Britain the rust is not severe in its effect on the cereal, but elsewhere the yield from a badly infected crop may be reduced by 50 per cent. or more. Bread (*vulgare*) wheats are rather more susceptible than the " hard " (*durum*) wheats, with the result that in America, where the rust can be very damaging, durum wheats are becoming more popular.

The life-cycle of this rust alternates between the cereal and barberry. The mycelium from within the shoot tissues of the growing cereal appears at the outer surface and bursts through the epidermis to form pustules. The hyphal endings in these pustules bud-off simple " summer spores," which are conidial in character and called *uredo-spores*. These uredo-spores are for the rapid spread of the fungus during summer. The uredo-spores, if autumn and winter conditions are not too severe, often over-

winter, and carry the fungus through the dormant period to infect the next year's crop.

As the host plant matures pustules containing a different kind of spore develop. These are on the same sites as the uredospores, or on new sites, but always, like them, confined to the leaves and stem. This second spore is two-celled and thick-walled. It is a resting or over-wintering spore, and is called a *teleutospore*. The teleutospore germinates in spring, and quickly produces small sporidia, which infect not a wheat plant but a barberry bush.

The mycelium in the barberry tissues soon forms small cup-shaped structures on the under surface of the host's leaves. From hyphæ in the base of these cups clusters of spores are budded off in long lines. These, called *æcidio-spores*, cannot infect the barberry, but only infect the alternative grass host.

No control of rust is possible except by interrupting the life-cycle. One obvious method of breaking the circle is to eliminate one of the hosts, the barberry. The eradication of barberry bushes as a preventative of rust was advocated by practical farmers long before the life-history of the fungus had been worked out. In certain states of America and elsewhere elimination of barberry and other plants, alternative hosts of other rusts, is insisted on by law.

The other method of interrupting the life-cycle is to grow a variety of cereal which is resistant to infection. It must be remembered in connection with such resistances that there are races within the fungus itself, and any one wheat variety is not immune to them all.

Yellow Rust

Another fungus related to black rust and also prevalent on wheat is yellow rust. This organism shows another facet of fungal life, for a wheat plant once badly infected with bunt becomes much more susceptible to yellow rust.

With all the rusts climatic conditions affect the success or failure of each of the various stages of the parasite, and therefore there are " bad rust years," and years when the incidence is less.

There is some evidence that a sexual act may occur in the life-cycle of some at least of the forms. The part involved in black or yellow rust may be seen in the upper surface of the barberry

leaf as a small flask-shaped structure sunk in the leaf tissue. This is the spermagonium, which may be a male organ ; it certainly produces small spore-like bodies, the *spermatia* or *pycnospores*.

Silver Leaf of Trees

No account of the fungi, no matter how brief, would be complete without some mention of those kinds which produce a fleshy "fruiting body" to bear the spores. The common mushroom might serve as an example, but as it is purely a saprophyte it does no damage in agriculture. An organism of this class which does cause disease is the one producing silver leaf in fruit trees. This fungus is often found as a saprophyte on the dead or dying stumps of broad-leaved trees such as poplar, beech, willow, and elm. In these situations fleshy fruiting bodies are developed. These vary considerably in size and shape, from little frilled brackets to quite massive shelf-like structures set close on the side of the tree trunk. The fruiting body has a hymeneal layer where basidia are massed. Each basidium produces four basidiospores. The vegetative mycelium is confined to the tissues of the host stem, principally in the wood. The hyphæ give out a soluble toxin, which, on being carried through the plant to the leaf, induces peculiar anatomical changes. The mesophyll cells of the leaf separate one from the other and from the epidermi, forming large intercellular spaces. These, filled with air, impart a silvery appearance to the leaf. This is a very good example of a fungus living in one part of a plant producing a toxin which shows its effect in another part of the host. There are no hyphæ in the affected leaf ; the whole mycelium is in the stem below. If an extract is made of the fungus, and this is carefully filtered to extract every living cell, silvering of the leaves will develop when it is injected into the stem of a healthy tree. All cases of silvering of leaves are not due to fungus. Insects and climatic conditions may produce a similar appearance. Nor does the fungus invariably produce silver-leaf as a symptom. The method of infection by this fungus is well understood. The basidio-spores, mentioned above, are produced in great numbers. These, when carried by the wind to a cut surface or wound on a tree, germinate, and the hyphæ produced spread rapidly through the wood. The growth of the mycelium is more rapid in a direction parallel with the longitudinal axis of the stem than it is transversely.

A branch once infected soon dies back. The fungus may spread through the whole shoot, and so the plant eventually succumbs. A very vigorous tree may "seal off" the fungus by forming a barrier of gum in front of the advancing mycelium. The pathogen cannot pass across this, and is isolated in the dead upper portion of the limb. If a branch showing silvered leaves be removed by a cut made well down towards the base the fungus may be excised.

All branches, alive or dead, bearing the fungus should be removed from the tree and burnt, for, as has been shown, this pathogen can live on saprophytically in the host it has killed. If the cut-off branches are left lying about near an orchard they will serve as a source of infection. Amongst the fruit trees attacked (apples and plums) some varieties are less susceptible than others.

Of all the remedial measures which may be employed against silver-leaf, cleaning up the orchard ranks high in effectiveness. In addition, all wounded surfaces, either accidentally caused or the result of pruning, should be sealed with a good oil paint with a white lead base. At pruning time the paint pot should accompany the pruning knife. Stockholm or gas tar both appear to be valueless as wound seals against silver leaf.

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SECTION FOUR

HEREDITY, EVOLUTION, AND CLASSIFICATION

PLANTS exhibit many features which they pass to their progeny. The study of the manner in which these characteristics are transmitted from generation to generation is the science of Heredity, or Genetics.

Because offspring tend to resemble their parents and each other, it is believed that plants which are alike are to some degree related to each other. In general, the greater the degree of resemblance the closer is the relationship assumed.

As plants have varied in particular features from time to time, they doubtless passed on these variations to their descendants. Lines of progeny receiving few or more of these variations diverged from each other in character though retaining many of the features of their common ancestry. In this way new kinds or races or classes of plant have evolved. Evolution is the study of the lines of descent of the types as we see them to-day.

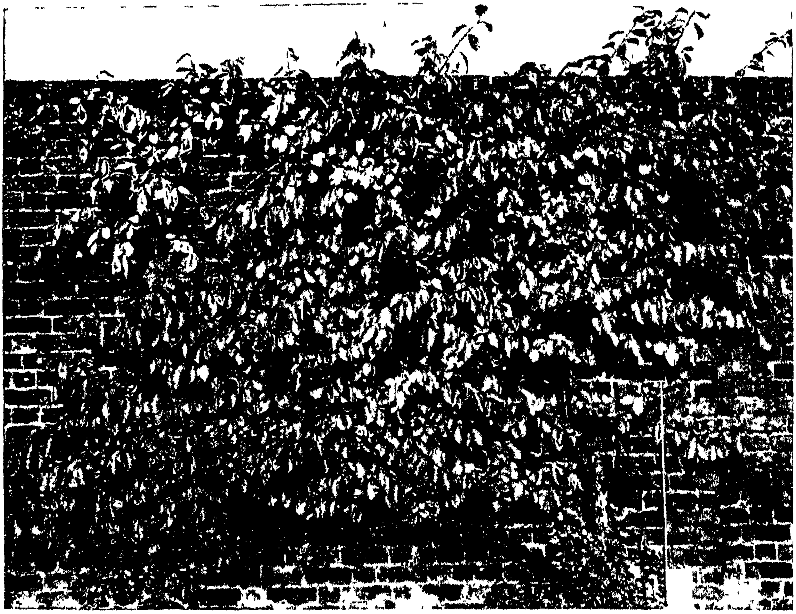
When plants are arranged or grouped according to their evolutionary relationship or descent they are said to be classified on a natural system. This is the method adopted by modern Taxonomy, or Systematic Botany.

PLATE FUNGUS SEASE BLACK RUST

(*Left*) Rust pustules on the stems and leaves of Oat. (*Centre*) Spores from the infected Oat have infected a Barberry bush. (*Right*) Pustules of spores on a leaf of Barberry. Through these an Oat plant will be infected

(*Photos : Plant Pathology Service, Dept. of Agric., Scotland*)

PLATE 118 FUNGUS DISEASE



Silver leaf on Plum. Note silvered leaves at top left

Leaves of Plum—those on right are silvered, on left are normal green
Wood of Plum bearing the "fruiting" bodies of the silver leaf fungus

(*Photos : F. T. Brooks*)

Chapter XXVI

HEREDITY AND PLANT BREEDING

The science of genetics, or heredity, is concerned with questions involved in the transmission, from one generation to the next, of all the attributes which gives each its individuality. In short, genetics seeks to explain why sometimes " like begets like," but at other times " begets the unlike."

The Causes of Differences between Plants

There are two classes of factors which condition the appearance and behaviour of the individual. On the one hand, there are the factors of the environment. One plant may be more favourably situated, getting more light, more manure or water, and because of this is bigger, leafier, or more productive. Another, less well favoured, suffering from paucity of supplies, imbalance of nutrients, or disease, is smaller or deformed or discoloured. The two plants, had they been grown under similar circumstances, might have appeared and behaved alike.

On the other hand, there are differences due to inheritance. There are tall varieties and dwarf varieties of peas ; wheat varieties with either white grain or red grain ; clover with hairy leaves or non-hairy leaves. The production of these characters is not due to factors of the environment, but to factors inside the plant which were transmitted to it from its parents.

Fluctuation and Variation

The characters of the plant, then, as we see them are the result of an interaction between the factors of environment and the internal, hereditable, or genetical factors. The action of the external factors is temporary, and produces only *fluctuations* in the course of development ; the internal factors are passed on to the next generation unaltered. The genetical factors are quasi-permanent units passing from generation to generation, and conditioning in each, definite *variations* between individuals differently endowed.

Where genetical questions are involved comparisons between

plants should be made only between individuals which have been treated alike, and therefore where variation and not fluctuation has been the cause of any differences between them.

Propagation v. *Reproduction*

Another point which must be clarified is the difference between propagation and reproduction. Propagation is the re-formation of a whole plant from a portion of the body of the " parent." Only body (somatic) cells are involved ; only mitotic or somatic cell divisions occur ; there is no fusion of nuclei. Hence, all the cells of the " daughter " plants are constituted or endowed exactly as the cells of the " mother," and contain the same set of factors. No matter whether the propagation is natural, as by runners, stolons, bulbs, corms, etc., or artificially produced by cuttings, grafts, buds, it involves only the splitting up of one body into parts and the establishment of these parts as separate entities. By propagation, *one individual* is distributed in time and space. For example, an apple variety, say "James Grieve," is bred only once. One tree is grown from a true seed. Every unit of "James Grieve " in the world is merely a part of the original tree, or a part of a part of it grafted on to appropriate roots. Similarly, with a commercial variety of potato, the variety is bred once, then tubers (branches of the body) are distributed. Units produced by propagation are called propagants, or clones. They are identical genetically, and, subject to fluctuation, identical in appearance.

Conversely, in reproduction the body cells of the parent do not enter into the process directly ; meiotic division comes between the somatic cell and the gamete, which in its chromosomes carries the genetical factors. The gamete is not constituted like the parental cell, though it derives its constitution from it. Further, in reproduction there is fusion of two gametes at fertilization to give the zygote from which the body of the new generation derives. The two gametes which fuse may have come each from parents of quite different genetical constitution, and so the offspring of the mating may not wholly resemble either parent but each in part.

Excluding the question of mutation which will be discussed later, propagation gives complete uniformity in the progeny ; reproduction holds out the chance of variation.

Crossing Plants

The genetical factors which pass from generation to generation must be carried in the gametes, the particular nuclei seen in the pollen grain and embryo sac.

To effect a cross between two plants, suitable pollen must be transferred from the stamens of one to the stigma of the other, precautions being taken that no other pollen is present. All being well, the pollen germinates and fertilization follows.

The two plants so "crossed" constitute the "first parental generation," or P1, and their immediate progeny, the "first filial generation," or F1. If the pollen supply used in fertilizing the F1 is restricted to its own spores, and it becomes self-fertilized or "selfed," the next generation is known as F2.

A Simple Cross

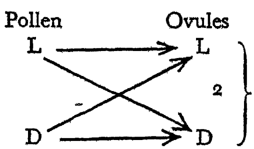
By appropriate crossing and selfing the behaviour in heredity of the different factors may be followed. A very simple case is seen in wheat. Some varieties have the spikelets arranged on the rachis, with an interval between. In others, the spikelets are placed quite close together and the "head" is compact. The one is said to have a "lax head," the other a "dense head." If two plants, one from each of these types, is crossed, the F1 is intermediate as regards this character. When the F1 is selfed, the F2 shows three classes of plant. In one class all the plants have lax heads ; in the second they are all dense ; while in the third they resemble the F1, and are intermediate in character. The cross is made either way, the dense head type or the lax head being used as the female, it matters not ; if sufficient plants are grown in F2, the numbers in the three classes will always bear the same numerical relationship to each other : 25 per cent. lax, 50 per cent. intermediate, 25 per cent. dense ; or the ratio 1 : 2 : 1. The behaviour may be shown diagramatically :

P1 Character	Lax head		×		Dense head
F1 Character			Intermediate		
F2 Character	Lax head	:	Intermediate	:	Dense head
F2 Ratio	1	:	2	:	1

The Gene

The mechanism which lies behind this segregation and recombination of factors is simple. It is now established that the genetical " factor " has a material basis in a piece of the structure of a chromosome. The name for this material basis of the theoretical factor is the gene. Each gene is known to occupy a definite place (the locus) in a definite chromosome. The chromosomes are paired bodies, and in a diploid (somatic) cell-nucleus there are two homologues, each carrying the members of the same gene pairs. The chromosomes of each homologous pair at meiosis part company. This means that every gamete will receive one chromosome from each chromosome pair, and therefore one gene from each gene pair. At fertilization the chromosome pairs, and therefore the gene pairs, are reconstituted.

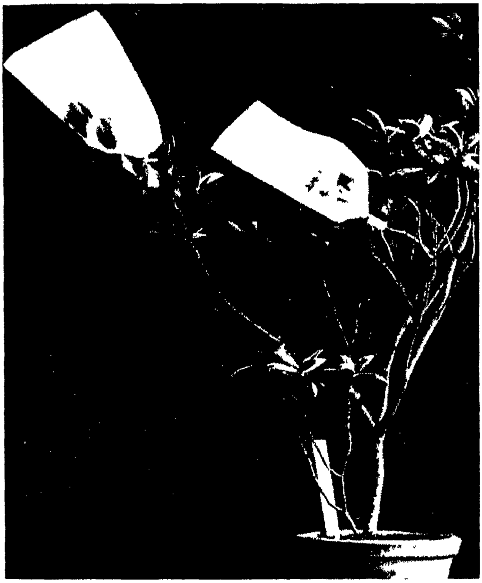
In the example just described the gene controlling the arrangement of spikelets on the rachis exists in two forms or potentialities. There is one potential for the lax condition, and the other potential for the dense condition. All the gametes of the lax parent will carry the gene for lax (L), and all the gametes of the dense parent will carry the gene for dense (D). These two different aspects of the gene pair meet at the fusion of the crossed gametes, and are therefore present in the somatic nuclei of the F1, where they exert their influence. When the F1 in its turn proceeds to form gametes the chromosome homologues part, and therefore the genes they bear part also. One half of the pollen will receive the gene aspect for lax, the other half for dense. Similarly, 50 per cent. of the ovules will carry " lax," and 50 per cent. " dense." On self-fertilization of the F1, it depends entirely on chance whether a pollen grain carrying " lax " meets an ovule carrying " dense " or " lax." Similarly for pollen grains carrying " dense," as there are equal numbers of dense and lax carriers in both the male and female gametes. The number of times each meets each in fertilization may be shown diagrammatically.



$$= \quad 1LL \; : \; \underbrace{1LD \; : \; 1DL} \; : \; 1DD$$

$$1 \; : \; 2 \; : \; 1$$

The manœuvres of the chromosomes at gamete formation and fertilization ensure the segregation and recombination of genes,



by excluding from the flowers all natural pollen-carrying agents. The most useful form of protection is the glassene paper bag

LAX V. DENSE HEAD IN WHEAT

Both heads have nearly the same number of spikelets but are of different lengths. Notice the space between spikelets in the lax head on the left and compare with the dense head on the right

PLATE 120 PLANT BREEDING

Parental (P_1) generation

First filial (F_1 generation

Second filial (F generation

" Iron " (awnless : white chaff) " April " (awned : red chaff)

The F_1 shows partial dominance of the awned gene. The gene for red is almost totally dominant. The F_2 shows the result of free segregation and recombination of both pairs of genes. (See p. 516)

(From material supplied by Sir Frank Engledow)

and therefore the character of the plants derived from the mating. This may be seen by expanding the scheme already given, and showing diagrammatically the chromosome pair which carries the gene pair involved.

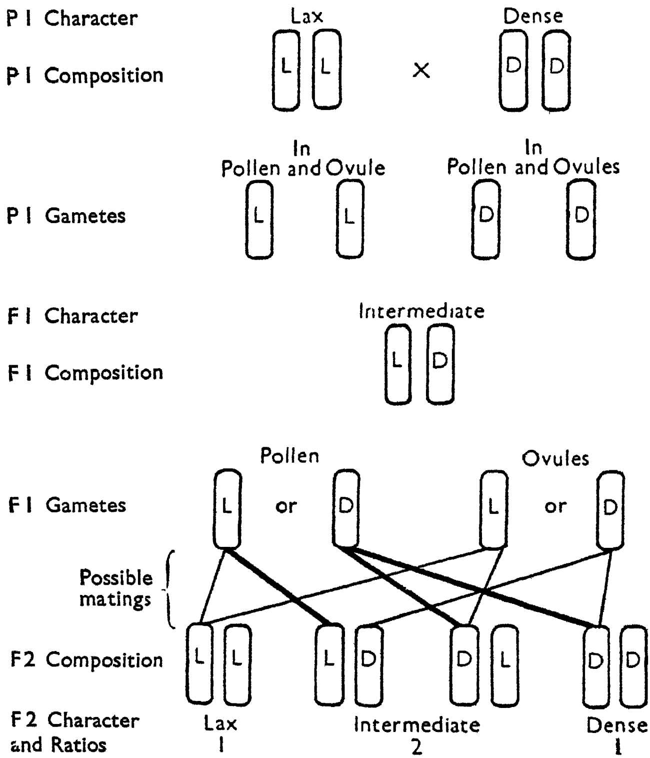


FIG. 175

The Heterozygote and the Homozygote

These hybrid plants whose somatic nuclei develop from a zygote containing both aspects of the gene pair (*e.g.* lax-producing and dense-producing) are known as heterozygotes, and are said to show the heterozygous condition. On the other hand, plants whose nuclei have two " doses " of the one aspect of the pair are homozygous, and such plants are homozygotes. The homozygote breeds true when self-fertilized, for all its gametes are alike. The heterozygote when self-fertilized shows segregation. That is to say, when it forms pollen and ovules the two aspects of the

gene pair part company and, depending how they meet for fertilization, produce plants of different character.

The essential point here is that gene pairs segregate at reduction division because their chromosomes segregate. They recombine at fertilization because at that point in the life-cycle the chromosome pairs are reconstituted. This explains why there are three classes in F2, and the fact that when large numbers are grown in this second filial generation the numbers in each class occur with the bounds of reassortment on the basis of pure chance in the ratio of 1 : 2 : 1.

Symbols for Genes

In dealing with such an experiment on paper the characters involved or the genes underlying them are represented by symbols. The usual symbol is the initial letter of the word describing the character. In the example just discussed " L " represents the gene for lax head, while " D " represents the gene for dense head.

This method is not good, as it does not indicate that L and D are members of a pair. In most writings both members are represented by the initial of one of them. The capital is used for one aspect, while the small letter is used for its " opposite number " or allelomorph. In the example just described " L " might represent lax and " l " dense. In examples yet to be described, the value of this will be more apparent.

Dominance and Recession

When other characters are considered in a hybridizing experiment, the F1 may not be intermediate but resemble one of the parents. For example, there are bearded wheats and non-bearded. That is, the " chaff " which envelopes the grain may have a long tapering awn (bearded), or this may be absent (beardless).

When a bearded wheat is crossed with a beardless one, the F1 is bearded. The gene for bearded dominates in the F1. It is said to be dominant to the non-bearded gene, which conversely is said to be recessive.

In F2 only two classes appear—beardless and bearded. The numbers of plants in these classes are in the ratio of 3 : 1.

In Plate 120 specimens from the actual plants in such a cross have been mounted in such a way as to illustrate the behaviour seen in a mating of this type.

In the lowest line of plants (the F2) it will be seen that there are twelve bearded plants to four without beards; that is, the numbers in the two classes are in the ratio of 3 : 1.

This is quite simply interpreted when it is remembered that one "dose" of bearded "swamps" or masks the presence of one dose of beardless. It is clear that the 3 : 1 ratio is merely the 1 : 2 : 1 with the first two classes amalgamated by the effect of dominance.

Only one plant (the homozygote) in every three of the bearded class will breed true. In this particular case the heterozygote produces much smaller awns than those borne by the homozygote. That is to say, one dose of the gene is not so effective as two. This partial production of the character is called partial dominance. When the heterozygote is quite similar to the homozygote the dominance is said to be total.

Phenotype and Genotype

A plant described on the basis of its external appearance is called the phenotype. If described by reference to the genes inside it is called the genotype. The F1 in this mating is phenotypically bearded, but genotypically bearded and beardless. In the F2, then, there are bearded phenotypes, some of which (the heterozygotes) are genotypically bearded and beardless, while the others (homozygotes) are phenotypically and genotypically beardless.

Test for Genetical Purity

In order to distinguish clearly between a homozygous and a heterozygous bearded, or, in other words, to distinguish between the two possible genotypes, the plants must be self-fertilized and bred-on. The progeny of the two genotypes will differ. On self-fertilization the homozygote produces only one class of plant, or, in other words, it "breeds true." On the other hand, the heterozygote segregates. This "proving" of the plant by reference to the character of its offspring is called the progeny test.

Where only a small number of plants can be grown, it may so chance that following on self-fertilization the recessive form does not happen to be produced. If, however, the suspected heterozygote, instead of being self-fertilized, is crossed with the pure recessive parental type, the chances of the recessive condition

appearing in the progeny is increased. Consider such a back-cross in the last-mentioned mating.

Every pollen grain from a beardless plant carries the gene beardless. This, supplied to a heterozygous plant, ensures that every ovule carrying the recessive gene will produce a beardless individual. In short, the cross of a heterozygote to the recessive ensures a 50/50 distribution in the two classes.

This is brought out when the mating is shown schematically:

Character of Back-cross P1	Bearded Heterozygote	×	Beardless Homozygote
P1 Composition	Bb		bb
P1 Gametes	Ovules		Pollen
	B or b		b
matings	B b		b b
progeny	Bearded 50%		Beardless 50%

Crossing back to the recessive parental type is a special case of progeny testing called the *back-cross.*

Mendel and Mendelism

The phenomenon of segregation and recombination of these genetical factors was discovered in the garden pea by Mendel. The ratios which he demonstrated are called Mendelian ratios, and the study of their various forms, Mendelism. Very many other but similar cases have been described in all sorts of organisms by many investigators. Sometimes dominance appears, sometimes the F1 is intermediate.

The Bi-Factorial Mating

When the parents of a cross differ in two pairs of characters, both showing dominance, four classes of plant appear in F2. This is due to two 3 : 1 ratios being superimposed.

This is brought out in Plate 120, already referred to in illustration of the inheritance of awns. Re-examination of the photograph will show that the left-hand awnless parent (variety Iron) has also white chaff (r) while the right-hand bearded parent (variety April) has red chaff (R). These two parents differ in two characters—awnedness and chaff colour. The F1 is seen to resemble

Diploid Tomato plant showing on right large-leaved tetraploid shoot

Left A diploid plant
Right A tetraploid. Both grown from cuttings of the plant above (*F. W. Sansome. Unpublished*)

A dwarf plant of Sweet Pea has developed a tall branch from cells in which the gene for height had mutated. Seeds from the tall branch gave talls and dwarfs ; one member of the gene pair had mutated. Tall is dominant to dwarf
(*From L. H. Stone, Journ. Genetics 26, 1932*)

PLATE NBREEDING MAIZE

Eight successive generations of Maize. Each one self-fertilized to provide the next. (Note progressive loss of vigour)
(Photo : Connecticut Agric. Expt. Station)

the "April" parent in that it is both bearded and red-coloured in the chaff.

When the F1 proceeds to form gametes the two pairs of genes involved segregate quite independently of each other, and therefore produce equal quantities of pollen grains in four different classes, each class differing from the others in gene content. Similarly there are four classes of female gamete. The classes may be defined in terms of their gene content as RB, rB, Rb, and rb.

The Punnett Chequer-Board

How the four classes of gamete will meet in self-pollination on the basis of pure chance is shown by a Punnett chequer-board. A square of sixteen small squares is drawn out and the genetical constitution of the male gametes (in pollen) is entered in the horizontal lines, and that of the female gametes (in ovules) on the vertical lines :

Pollen ⟶

Ovules ↓

	RB	rB	Rb	rb
RB	RB RB	RB rB	RB Rb	RB rb
rB	rB RB	rB rB	rB Rb	rB rb
Rb	Rb RB	Rb rB	Rb Rb	Rb rb
rb	rb RB	rb rB	rb Rb	rb rb

The chequer-board gives all the possible combinations, and using initials to represent the *characters* of each the phenotypes formed are as follows :

RB	RB	RB	RB
RB	rB	RB	rB
RB	RB	Rb	Rb
RB	rB	Rb	rb

The totals for each combination are also shown :

	RB	rB	Rb	rb	
First row . . .	4	—	—	—	
Second row . .	2	2	—	—	
Third row . .	2	—	2	—	
Fourth row . .	1	1	1	1	
Total . .	9	3	3	1	=16

This mating may now be shown in full, diagramatically as :

	Iron ×	*April*
P1 Character	Beardless and White Chaff	Bearded and Red Chaff
Composition	bbrr	BBRR
Gametes	br	BR

F1 Character	Bearded and Red Chaff
Composition	BbRr
Gametes	RB Rb rB rb

F2				
Character	9 Red and Bearded	3 Red and Beardless	3 White and Bearded	1 White and Beardless
Composition	1 RRBB 2RrBB 2RRBb 4RrBb	1RRbb 2Rrbb	1rrBB 2rrBb	1 rrbb

It will be noted that only four out of the sixteen possible genotypes breed true, namely, those whose constitution appears on the diagonal line joining the top left-hand square with the bottom right-hand square of the chequer-board.

In the field the true breeders can be separated from the heterozygotes only by a progeny test or a back-cross. Of course, the ultimate recessive (rrbb) needs no such test ; nothing is here masked.

With three or more character pairs involved, the results are equally easily analysed and forecast.

The Gene on the Chromosome

A plant shows hundreds of units of character and must therefore have hundreds of pairs of genes, yet it has only a limited number of chromosomes in each nucleus ; for example, in bread wheat there are twenty-one pairs in the soma or twenty-one individuals

in the gamete. Many other plants have fewer chromosomes, yet these bodies have to carry all the genes.

It is known that each chromosome carries a number of genes, and these are distributed up and down the chromosome in linear order like beads on a string. Each chromosome always carries the same gene set. The distance between neighbour genes on a chromosome is constant, and the order in which they occur from one end to the other never varies in normal cases.

Linkage

This leads to some amendment of the ideas suggested above, for if two gene pairs are located on the same chromosome they will not segregate independently. They are said to be " linked " or show linkage. Linked genes tend to come out of F1 into F2 in the relationship they went into the F1 from the P1. This is shown in Fig 176. Suppose the genes for two character pairs to be represented by Aa and Bb. If these are on different chromosome pairs they will segregate freely and give a normal 9 : 3 : 3 : 1 ratio in F2. If, however, the two pairs of genes are on one pair of chromosomes they will not segregate freely. If the linkage is total, the F1 will produce only two kinds of gamete, and not more than three classes of phenotype will occur in F2. Free segregation is not possible when the different gene pairs are in the same chromosome pair.

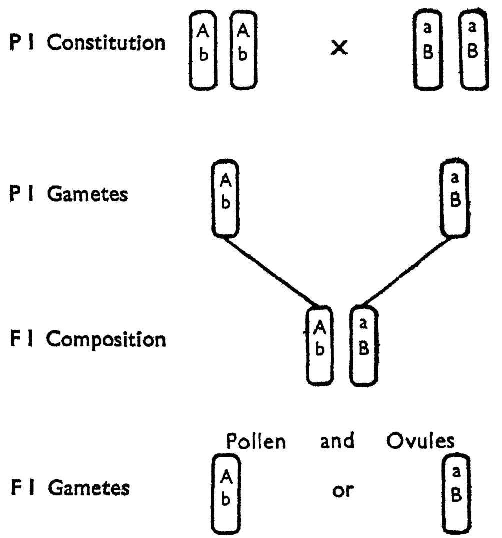
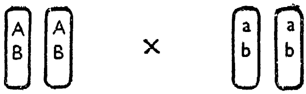


FIG. 176

If both dominants come in from one parent and the recessives from the other as—

Fig. 177 

then there will be only two classes of phenotype in F 2.

Crossing-over

Linkage would prohibit the possibility of new combinations being bred, were it not for the fact that at syndesis in meiosis, the chromosomes of homologous pairs become closely intertwined, and in separating give the appearance of having broken and united with an exchange of parts between the two members of a chromosome pair. The points where they cross-over each other in the intertwining, called a *chiasma*, can be seen under the microscope. The actual mechanics of crossing-over are complicated, but its general effect may be shown in the rather simplified diagram below (Fig. 178).

On the left is the original chromosome pair ; next the two intertwined ; next the two chromosomes are shown reformed with exchange of parts, while on the extreme right are the chromosomes as they go forward to complete mieosis and pass to the gametes.

This diagram illustrates cytological crossing-over. Genetically, this results in the appearance of four classes in F2, but the ratio of these classes is not the expected 9 : 3 : 3 : 1 because free segregation is interfered with there will be a deficiency of two of the classes and increase in the others. In short, linkage restricts segregation of genes ; crossing-over permits partial segregation.

The amount of crossing-over between any two genes on a chromosome is proportional to the distance along the chromosome between them. The greater the length of the chromosome extending between two loci the greater the chance of a cross-over point (a chiasma) occurring.

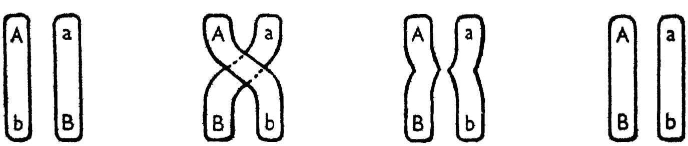


Fig. 178

Variability of a Gene: Mutation

It may be asked now how a plant comes to have two aspects of a character or how a character pair comes to be. It is known that the wild-type gene as it occurred originally may alter its nature. The alteration produces a new expression of the character. The process, or act of alteration, is called mutation. The new type of plant so produced is called a mutant or a mutation.

A gene in the majority of cases mutates only once, and thus gives a character pair, the wild type and the mutant. The same gene, however, may mutate again and give three forms of the gene—the original wild type and two mutants. This provides three expressions of the character. Only two of these three can be present in any diploid somatic nucleus, and only one in any gamete.

A case may be taken from the haricot bean, plants of which may have green foliage and green pods (Gr) or green foliage and yellow pods (G), or yellow foliage and yellow pods (g). When Gr is crossed with G, the F1 shows green pods and foliage. The Gr condition is dominant to the G condition. When the G type is crossed with the g, the green foliage and yellow pods condition is dominant. Thus we see a series of decreasing dominance—Gr dominant to G, and either of these dominant to g. Such a graded set is called a multiple-allelomorphic series.[1] All sorts of quantitative and physiological conditions are known where the genes for the characters belong to such a series. In some series there may be more than three aspects, for cases are known where the gene has mutated five or six times, and six or seven character expressions exist.

The Heteroploid

Another aspect of cytology affecting Mendelian ratios must now be referred to. It sometimes happens that at mitotic or meiotic division the daughter nuclei do not separate cleanly in the usual manner. In these cases the chromosomes, either as a whole set or as part of a set or even individual members, lag behind. The laggards which should have gone to one daughter nucleus are

[1] The term allelomorph is practically synonymous with factor, and was used to describe a factor pair because one was the " mirror image " of the other.

included in the other. When this occurs, nuclei are formed with a number of chromosomes different from that normally found in the species. A nucleus with such an aberrant number of chromosomes or a plant in whose nuclei they occur is said to be heteroploid.

If a whole chromosome set is replicated, the heteroploid is said to be balanced or *euploid*. If only a part of the set is replicated, the nucleus is of the unbalanced or *aneuploid* class. Most attention is directed to those cases where whole sets are concerned, that is, to the euploid form. Where one replication of the normal diploid has taken place, and the homologues are in threes, the plant is said to be *triploid*. Where the diploid has doubled and the homologues are in fours, the plant is said to be *tetraploid*. Plants are known where the body cells contain only half the normal diploid number ; that is, the number normal to the gamete of the species. These plants are known as *haploids*. There is thus an ascending series in the terminology : haploid, diploid, triploid, tetraploid, pentaploid, hexaploid, and upwards.

These have been formed in nature as the result of some unknown stimulus, or artificially in cultivation by the use of such drugs as colchicine.

The Effects of Heteroploidy

Giantism.—Replication of chromosome sets often results in the production of a bigger (giant) form of plant. This in itself may be very useful as, for example, when it occurs in a plant of a forage crop.

Sterility and Fertility.—Heteroploidy may be very useful in regard to sterile hybrids. These hybrids often result from crosses between plants which are not very closely related, but close enough to form a new hybrid plant. The chromosomes derived from the two parents are sufficiently homologous to form a mixed nucleus in F1, but not so as to behave normally at meiosis. The hybrid fails to form viable gametes. Such hybrids or " mules " are sterile, and therefore, unless they can be propagated successfully and economically, are of little or no use in practice. Replication of the mixed sets of chromosomes, if it occurs in such a sterile hybrid, may render it fertile.

One of the clearest examples of this is furnished by a non-agricultural plant. *Primula verticillata*, with nine pairs of chromo-

somes in the somatic nuclei, can be crossed with *Primula floribunda*, which also has nine pairs of chromosomes. The gametes of each, therefore, contain nine chromosomes, and these form the hybrid. None of the nine floribunda chromosomes are homologous with the nine verticillata members, and therefore successful meiosis in the hybrid is barred. Viable gametes are not possible, and the plant is sterile. The sterile hybrid formed a euploid and immediately became fertile. Schematically, the mating and its results are shown below, the chromosomes being symbolized by the initial letter of the species from which they are derived.

Parental mating	9V V	×	9 F F	
Gametes	9 V		9 F	V and F chromosomes are not homologous and the F1 plant is sterile.
F1		9 V 9 F		
		Heteroploidy occurs		
New heteroploid hybrid		9 V V 9 F F		Each V chromosome has now a homologue, so has each F chromosome. Meiosis is possible, and fertility ensues.

By replication, each V chromosome obtains a homologue and similarly each F chromosome. Normal meiosis is possible and gamete production follows.

Many species not closely related can form hybrids which are sterile. It is probable that many of these will be rendered fertile when duplication occurs.

Wide crosses as between, say, a wild grass like couch and wheat, or between turnip and cabbage, are important because the new gene complex brought into being results in more than a mere addition of the characters of one parent to those of the other. Genes even in a normal diploid soma interact on each other to some extent, and when two complete gene complexes interact the effect is greatly increased, so that a new plant different from both parents is brought into being. This is paralleled in chemistry when, for example, the union of sodium, a white silvery metal, with chlorine, a green gas, produces a new substance, sodium chloride with characters quite different from the parent substances.

Natural Hybridity and Heteroploidy

The formation of heteroploids has occurred in nature. For example, our modern bread wheat as it was evolved is a complex hexaploid of diverse parentage with three sets of seven, that is, twenty-one, chromosomes in the gamete, and twenty-one pairs (forty-two individuals) in the somatic nucleus.

One interesting result of heteroploidy occurs when the component sets of chromosomes each contribute to the new plant similar genes.

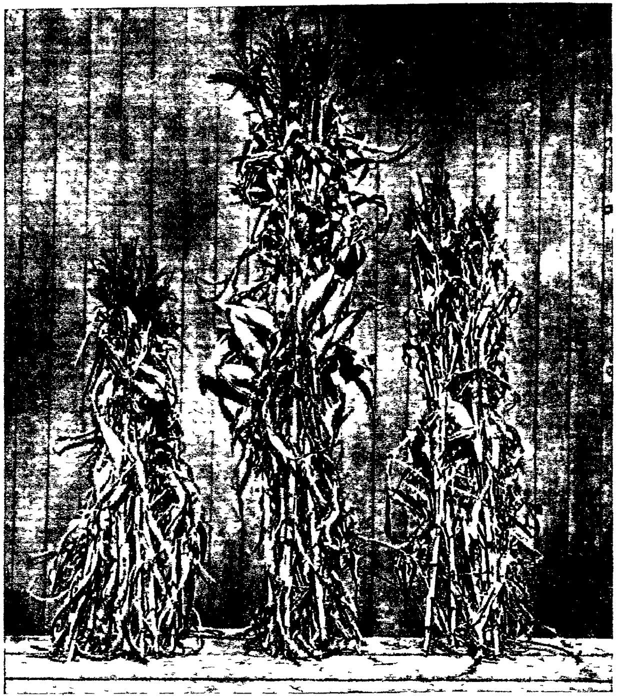
A case in point arises in connection with the production of the red colour in the grain of bread wheat. Here, if an appropriate variety with red grain is crossed with a variety having white grain, a 3 : 1 ratio red : white is obtained in F2. If a different red-grained variety had been used as a parent, a 15 : 1 ratio red : white in F2 would have been obtained. If yet another variety had been employed, the ratio of red : white in F2 would have been 64 : 1. Results such as these indicate that three pairs of genes are involved in the production of grain colour. Furthermore, each pair must be located on different chromosome pairs, because the genes segregate and recombine freely. In short, there must be six chromosomes (three pairs) in each hexaploid somatic nucleus, all of them carrying a grain-colour gene. Cytological evidence shows the bread wheat to be hexaploid. If the three gene pairs be represented by R/r, R_1/r_1, R_2/r_2, then the recessive white grain must be rr, r_1r_1, r_2r_2. The red parent of the example providing a 3 : 1 ratio in F2 must be one of the following, RR, r_1r_1, r_2r_2, or rr, R_1R_1, r_2r_2, or rr, r_1r_1, R_2R_2. The red grain parent in the cross giving the 64 : 1 ratio has the constitution R_1R_1, R_2R_2, R_3R_3.

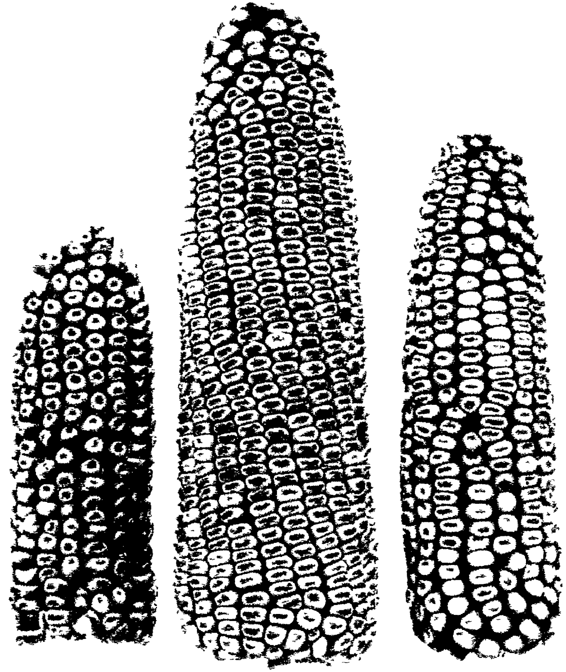
Multiple genes (polymeric series) of this type become important when they affect quantitative characters, and each dose of, say, the dominant produces an increase in the character. Sugar content of sugar beet depends on a set of replicated genes, and every additional " dose " of gene produces an increase of sugar content.

Plant Selection

Cytological aberration and genetical hybridity provide plant populations variable in character. Variation in a crop, no matter how induced, provides the plant selector with his material. A

PLATE 123 HYBRID VIGOUR IN MAIZE





Two inbred strains of Maize on either side of the vigorous hybrid got from their mating. (*Left*) The plants in flower. (*Right*) The ripe grain (cobs)

(*Photo : Connecticut Agric. Expt. Station*)

PLATE 124 HYBRID VIGOUR

Commercial production of hybrid vigorous (heterozoic) seed maize, three rows of the strain to be used as female (seed) parent alternate with single rows of the strain to supply pollen. The male inflorescence is removed from the seed parent

(Photo : Connecticut Agric. Expt. Station)

new combination of genes or gene complexes can be the starting point of a new variety waiting to be selected and multiplied. There are three methods of selection.

Single Plant Selection : Pure Lines

The first consists of selecting single plants, self-fertilizing them, and maintaining the progeny of each as a separate "line." In effect this subjects each selection to the progeny test. The best line which breeds true can be retained and the others scrapped. This method is known as single-plant selection. If the original parent was homozygous for the characters observed, a non-varying or *pure line* will have been formed. A pure line consists of the descendants of one homozygous individual, self-fertilized and never cross-fertilized. This amounts to *genotypic* selection.

A line pure for *all* genes is probably not possible, but a line pure in all the genes that matter is obtainable in practice. It is to be noted that, so far as concerns the genes for which the line *is* pure, further selection can have no effect. A pure line, then, by definition is non-varying. Apart from environmental fluctuation and the possibility of mutation, no alteration in appearance or behaviour is possible.

Mass Selection

The second method of selection is to choose all the plants in a crop which appear to conform to a predetermined standard. Such is mass or *phenotypic* selection. This is often useful with plants which are individually self sterile, or where the character is quantitative and depends on a comparatively large series of polymeric genes. Mass selection gives an immediate effect with a large bulk in the first generation. As generation follows generation, if re-selection is not practised on each, the effect wears off, and the strain "runs back" to an average. Consider a plant in which yield is conditioned by five quantitative factors :

$$Y_1Y_1 \quad Y_2Y_2 \quad Y_3Y_3 \quad Y_4Y_4 \quad Y_5Y_5$$

Such a plant with all genes in the positive condition would give maximum yield. Fluctuation, however, will mask the difference between such a plant and others, as :

$$Y_1y_1 \quad Y_2Y_2 \quad Y_3Y_3 \quad Y_4Y_4 \quad Y_5Y_5$$
$$Y_1Y_1 \quad Y_2y_2 \quad Y_3Y_3 \quad Y_4Y_4 \quad Y_5Y_5$$

and so on. In short, phenotypic selection will not differentiate between small differences in genotype. All these genotypes freely intercrossing will in a few generations redistribute the low production gene through the crop, and a plant of, say, the constitution y_1y_1, y_2y_2, Y_3Y_3, Y_4Y_4, Y_5Y_5 develop. The total yield will recede as the years pass, and the strain is said to " run back." Mass selection gives a large yield of an improved strain quickly, but the stock must be re-selected each year.

Mass selection is often possible on large-scale lines. For example, in many countries growing crops are inspected officially, and where a crop conforms to a definite standard the grower receives a certificate for it. When such a certification scheme is widely patronized it amounts to a large-scale mass selection.

Roguing

The third method of selection is not to select out the good plants, but to pick out from a crop the wrong ones or " rogues." These are the plants which do not conform to standard.

Roguing has a potent influence when the rogue is due to a dominant gene, and when the desired character is due to a recessive. Roguing out a recessive is not really effective in practice, for it leaves in the crop the heterozygotes. In this latter case it usually pays better to develop a pure line following a progeny test.

STERILITY

Self-fertilization and cross-fertilization have been referred to. These are often barred by sterility. Almost any cabbage plant will illustrate the point. If its own pollen only is allowed access to its stigmas a cabbage will set few or no seeds. If pollen from other cabbage plants gets access to the stigma, fertility is complete. This proves that its ovules are fully functional. Its pollen is fully effective in producing seed on most others of its fellows. The gametes of the plant accordingly are fully viable but self-incompatible.

These compatibility relationships are controlled by a set of multiple allelomorphs, usually designated S_1, S_2, S_3 . . S_7. It is now known that the tube of a pollen grain carrying any S allelomorph can hardly pass through a style carrying this same

allelomorph in the pair resident in the cells. This is shown diagrammatically in Fig. 179.

A similar mechanism affects many varieties of fruit tree. If an orchard has been planted only with such a self-incompatible variety, every one of the trees produced by vegetative propagation will have exactly the same gene complex. Hence, every stigma will contain incompatible genes in common with the pollen supply and fertility will be barred. Such an orchard must be interplanted with a few trees of another variety which is known to be capable of supplying suitable pollen.

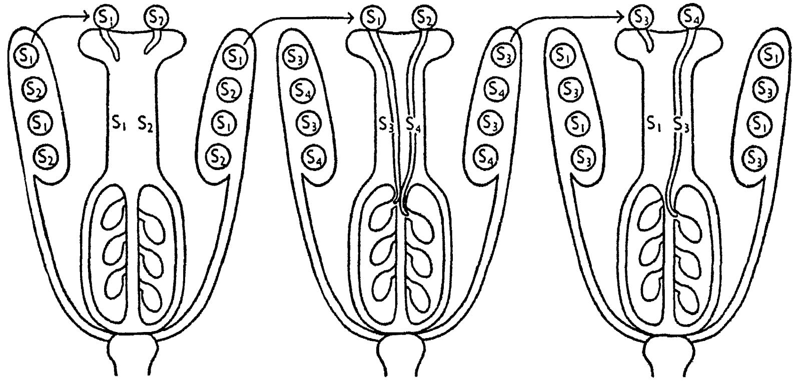


FIG. 179

Self and Cross Compatibility

If either of the two possible allelomorphs in the cell nuclei of the tissues of the style are identical with the one in the nuclei of a pollen grain, that pollen grain will not penetrate through the stylar tissues and effect the fertilization of an ovule

Many plants are known to have a cytological constitution which does not permit of normal meiosis. The plants are usually of hybrid origin. Many fruit trees are of this nature and do not form viable gametes.

LOSS OF VIGOUR

Where sterility is no bar, and continued self-fertilization is practised, another disability may show itself. The vigour of the progeny derived through continued self-pollination falls progressively generation by generation. In maize, for example, after a few generations of self-fertilization the inbred lines become weak, and in extreme cases may fail completely and die out.

Hybrid Vigour or Heterosis

Curiously, when two inbred but unrelated lines are crossed the F1 is often extremely vigorous. Out-breeding brings back vigour. This vigour in a hybrid has been called *heterosis* or *hybrid-vigour*. It shows only in the F1 and does not appear in F2 when the F1 is self-fertilized. When appropriate inbred lines are used as parents, the F1 is often very much more vigorous and yields much more than any commercial lot. Heterozic or Heterozygous maize seed is now sold for crop production in the United States of America. In fact, for this crop, practically all progressive growers sow only hybrid vigorous seed. All of the F1 crop goes for consumption as food, etc. ; none is retained for sowing. Each year the F1 is made anew from inbred parental lines which are known to give the maximum effect when crossed.

The commercial production of heterozic maize seed is simple. The two parental lines are interplanted in rows. At flowering time all the male inflorescences are removed from the plants designed as the seed parent. It is therefore pollinated only by its neighbour, and all the " seed " produced by it is of hybrid origin.

In any crop produced by vegetative propagation the vigorous hybrid need be produced only once. All clones are genetically identical and just parts of the F1 itself. They retain all its characteristics in full effect. This is well seen in the poplar tree used for wood pulp. Two parents are crossed. If the progeny is highly vigorous, suckering is induced. The suckers are planted out. The trees from such suckers grow very fast and harvest is brought nearer by a number of years.

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CHAPTER XXVII

THE CLASSIFICATION AND IDENTIFICATION OF PLANTS

THE best way to get to know plants so that they may be readily identified and named is to see them often. They should be seen fresh in the field or dried and preserved in a collection or herbarium. The vast range of different plants seems confusing at first, but when they are properly arranged they fall into a systematic classification.

SYSTEMATIC BOTANY

The systematic arrangement adopted and used to-day is a natural one. That is to say, the different plant forms are arranged in groups, the members of each group being related to one another. It is assumed that the more two plants resemble one another, the closer they are related. In short, it is accepted that all plants with many characters alike are related, and have descended in evolution from a common stock or ancestor, each inheriting from this source some of the original characters. Thus all flowering plants are more closely related to one another than any of them is to a non-flowering plant. Two great classes are so formed, the flowering plants, or *Phanerogams*, on the one hand, and the non-flowering plants, or *Cryptogams*, on the other.

THE FLOWERING PLANTS

The flowering plants may be subdivided into two. There is a less highly evolved section in which the carpel leaf is open and the ovules left exposed. These are the *Gymnosperms* and include the pines and firs. In the more highly evolved flowering plants, the *Angiosperms*, the ovule is protected in a closed box or ovary formed from the infolded carpel(s). All our agricultural crop plants and the vast majority of our weeds are angiosperms.

The Angiosperms

The angiosperms may easily be divided into two classes. Those with one seed-leaf or cotyledon, the monocotyledons, and those with two embryonical leaves, the dicotyledons. The monocotyledons and dicotyledons probably diverged early in

evolutionary time, and therefore show quite a number of other major differences. These may be listed :

	Monocotyledons	Dicotyledons
Root	Root produced from radicle not persistent. Root system of mature plant adventitious and consisting of many members of equal size.	The tap-root produced from radicle persists, and in an undamaged plant grown from seed is a portion of the main axis.
Shoot	Tends to have a number of shoot members all of equal girth.	Tends to have a main axis with branches of subordinate character.
Leaf	Venation shows a number of veins all equal in size and thickness, none anastomosing.	Veins form an anastomosing network.
Flower	Parts in threes or multiples of three (only in a few in fours) as sepals 3, petals 3, stamens 3 + 3, carpels 3.	Parts of flower in fours, fives, or multiples thereof; *e.g.* sepals 5, petals 5, stamens 10, carpels 5.
Anatomy	Bundles of root 10 or more. Bundles of shoot many and, as seen in T.S., scattered and immersed in ground tissue. No cambium present in root or stem, hence no secondary thickening.	Bundles of root, 4 or 5. Bundles of shoot few and arranged in a ring in a definite stele. Cambium invariably present, hence always the possibility of secondary thickening.
	Closed bundles.	Open bundles.

If the flowering plants of a parish, district, or country are listed, or specimens of them filed in a herbarium in these two classes alone, some degree of order appears out of chaos.

By paying attention to other characters, particularly those of flower structure, it is possible to arrange the plants in smaller and smaller groups. The members in each smaller group show in succession a greater degree of likeness (relationship) one to the other than any of them shows to a member of any other group.

Plant Names

By this process of subdivision into more homogeneous groups, each subsidiary group becomes smaller and smaller until the individual is reached. The individual in this sense is really composed of many plants, all of which are identical apart from fluctuation and minor genetical characters. This unit, called a *species*, is practically homogeneous and receives a name.

The name in common use usually describes the plant to some extent : for example, " eyebright," with its small flowers like bright eyes ; lungwort, because the leaf marking resembles lung tissue ; sweet pea, from the scent and pea-like flower, and so on. Unfortunately, these " common " names differ in different districts or areas. The plant known as " Creeping Thistle " in Britain is known as " English Thistle " in America, " Californian Thistle " in Australia, and by very many other names in non-English-speaking countries. A name universally used for the same species all the world over is required. Science is international, and scientists must be able to write and speak about a plant so that scientists everywhere can understand just what particular plant is meant.

The Systematic Name

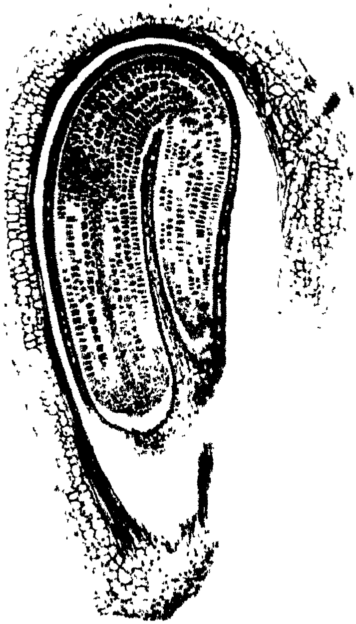
When naming a newly discovered plant, a botanist describes it very accurately in Latin and files a specimen of it in a herbarium. This is the type specimen. The description is published, and the relationship of the plant to other already named plants indicated. On this relationship the plant takes its appropriate place in a list of plants called a " Flora."

Genus and Species

The name given to it by its first describer will be in Latin or a latinized form, and consist of two words. The first of the two words composing this binomial is the generic name, and shows the genus or near relationships of the plant, and is sometimes regarded as the equivalent of the surname or family name in human affairs. The second part of the plant binomial is the specific name. It is peculiar to that species, and is sometimes looked upon as the equivalent of the baptismal or " given " name of a person ; it marks the plant off from all its immediate relatives.

Varieties

The plant known variously as white clover, Dutch clover, wild white, ladino clover, and so on, is known to botanists as *Trifolium repens*. *Trifolium* applies to all the plants with similar flower structure and all having leaves of three leaflets. Most of the plants commonly referred to as clovers belong to the genus



MONOCOTYLEDON

The embryo is the hook-shaped structure inside the testa. To the left the radicle points downwards. The cotyledon is bent over to point downwards on right. The plumule is to the left at the apex of the radicle

DICOTYLEDON

L.S. of embryo. Pointing downwards is the radicle. At its apex is the plumule. The two long, strap-shaped cotyledons are inserted to right and left of the plumule

LUNGWORT

The leaves of this plant suggest the appearance of lung tissue. From this the plant received its name. The botanical name *pulmonaria* refers to the same feature

Trifolium. The specific name, *repens*, is applied to the special creeping type with white flowers grouped in a head borne on a long stalk. Anyone with experience of white clover will know that in practice ladino white is different from Dutch white, and both of them are different from wild white. Close examination of the three will show that ladino is just a giant form of Dutch, and apart from the size there is no real botanical difference. Again, there is no botanically significant difference between wild white and Dutch or cultivated white, except that wild white is longer-lived, not so free-flowering, etc. In short, within the species we recognize minor differences called *varieties*. Just as in garden plants we recognize, say, a pink-flowered variety of sweet pea as against a white-flowered variety, yet both are sweet peas.

Strains

Amongst agricultural plants the varietal differences are based on observable features such as colour of skin in turnip, or shape of tuber in potatoes. When two populations of a species look alike and cannot be told apart except that the members of them *behave* differently, say when one lot resists disease and the other does not, the two are said to be different *strains*.

The kind of difference which constitutes the gap between a strain and a variety is fine ; so, too, is the demarcation between a variety and a species. Some botanists tend to regard as species plants showing the finest of differences. Others would lump into one species all plants reasonably well related. A strict definition of what is meant by a species is not possible, and in practice the degree of variation permitted within the unit depends on the personal opinion of the botanist concerned.

The point here is that all plants included in a genus are so placed because on a given set of characters they show considerable resemblance. The species within the genus are separated from each other on differences in other but less important characters. The number of species which may occur within a genus is not constant. For example, there are some twenty-one species of true clover (*Genus Trifolium*) common in Britain, while there are only three in the closely related genus of the sweet clovers (*Melilotus*). The number depends fundamentally on how active the process of variation has been in the history of the genus and how long it has been going on.

THE NATURAL FAMILY

In discussing plants, the genus is usually a convenient unit to refer to, but often a broader picture is necessary. Hence all genera showing a degree of relationship on major characters are arranged into the larger units of the Natural Family. Thus clovers (*Trifolium*), sweet clover (*Melilotus*), peas (*Pisum*), beans (*Vicia*), haricot beans (*Phaseolus*), and all others having flowers of the very typical pea-type are included in the Natural Family *Leguminosæ*.

Families may be arranged in still larger groups. For example, all Families having the petals not grown together are grouped in *Polypetalæ*, as opposed to those where the petals are all fused, the *Gamopetalæ*.

THE USE OF A FLORA

Before attempting the accurate identification of plants, the student should procure a complete list of the species expected or known to be in the district. This list (with detailed descriptions of each species) arranged in Families and Genera is called a Flora of the area. By " area " is meant perhaps a parish, a county, a country, or even a continent. The *British Flora* compiled by Bentham and Hooker covers the whole of the British Isles. If in addition to a suitable flora illustrations of the plants or an authoritative herbarium are available they will prove of great assistance in identification.

The method with an unknown plant is, first, to assign it to a major unit, and then follow it down to lesser groups. Dicotyledon or monocotyledon is soon decided. To get to the Natural Family the use of a " key " may be necessary. A key is merely a table composed of pairs or trios of contrasting questions. As the plant answers to one or other of the pair the student passes to another pair until the plant is " run down." For example, the first three pairs of questions in Bentham and Hooker's *British Flora* run :

1	Flowers compound consisting of separate florets in a common involucre, anthers joined	(2)
	Flowers distinct or if in a head having anthers free	(3)
2	Ovary and fruit containing a single seed and appearing like a seed under the floret	Family Compositæ
	Ovary and fruit 2-celled with several seeds	Jasione
3	Perianth double, consisting of a calyx and corolla	(4)
	Perianth single or none	(85)

Keys may be useful in getting quickly to the Family. It is advisable, however, that the general characters of each of the families commonly found should be familiar to the student, so that an unknown plant, a member of one of them, is then quickly recognized as such. A key similar in construction is provided for each of the genera. This directs the student to detailed descriptions of individual species and varieties with which his specimen may be compared.

As each species in the district is found and named, it should be pressed, mounted, and added to a private herbarium. By collecting, naming, and filing the plants, familiarity with them is acquired, and soon the use of keys may be dispensed with.

Classification of Cultigens

The natural system just described is quite satisfactory when dealing with wild plants and weeds; with cultivated plants (cultigens) difficulties arise. Descriptions of the various types based on purely morphological data leave out much of importance. It does not include the more important facts based on the so-called physiological characters. For example, it is quite possible to have two varieties of wheat, morphologically alike, but agriculturally totally dissimilar. One might be a spring type suitable for a warm climate with rich soil; the other, quite the reverse. A full description of the plant must include many facts in addition to mere morphology. The kind of information usually required falls under some eleven heads:

(1) The length of the vegetative period
(2) The length of the development phases and their rhythm
(3) Definition of economic characters, such as size and weight of fruits and seeds, the total yield per plant per unit of area
(4) Vegetative characters (stoloniferous, rhizomatous, bulbous, etc.)
(5) Ability to resist drought
(6) Ability to resist cold
(7) Nature of the flowering mechanism
(8) Resistance or susceptibility (if any) to attack by specified diseases and insects
(9) Sterility/fertility relationships

(10) Ecological type of the plant. Xerophytic, hydrophytic, mesophytic, etc.
(11) Data relative to the numbers, behaviour, and ultimate source of the chromosomes

The work of collecting all these data for each cultigen might seem insuperable, but knowing the natural habit of a plant, many of the characters can be assumed. In any case, description based on morphological data must be always the point of departure for any of these more elaborate systems of fuller description.

The Methods by which Plants Vary

The mechanism which provides new variants, whether the differences are small or great, or occur in nature or under cultivation, are always one or other, or perhaps a combination, of two or more of the methods outlined under plant breeding, viz.

(1) Gene mutation
(2) Replication of identical chromosome sets, auto-heteroploidy
(3) Hybridization between plants of differing gene content but without cytological replication, then followed by segregation and selection
(4) Hybridization followed by chromosome replication, allo-heteroploidy

The Vegetable Kingdom

The flowering plants are undoubtedly the most important group the agriculturist has to deal with, but it is desirable to see their connection with the other members of the vegetable kingdom. Using the thesis of evolutionary descent, it is comparatively easy to trace the line back downwards from the most highly evolved angiosperms. The group less highly evolved is the gymnosperms with the seed exposed. The two groups gymnosperms and angiosperms, together form the great division of the seed plants, *spermophyta* or *phanerogams*.

The seed comprises parts derived from three distinct phases of the recurrent life-cycle. The soma or spore-producing (sporophyte) phase of the parent provides the testa, etc. The gamete or "n" phase (gametophyte) leaves in the seed relics of antipodal cells, etc., while the somatic or sporophyte phase

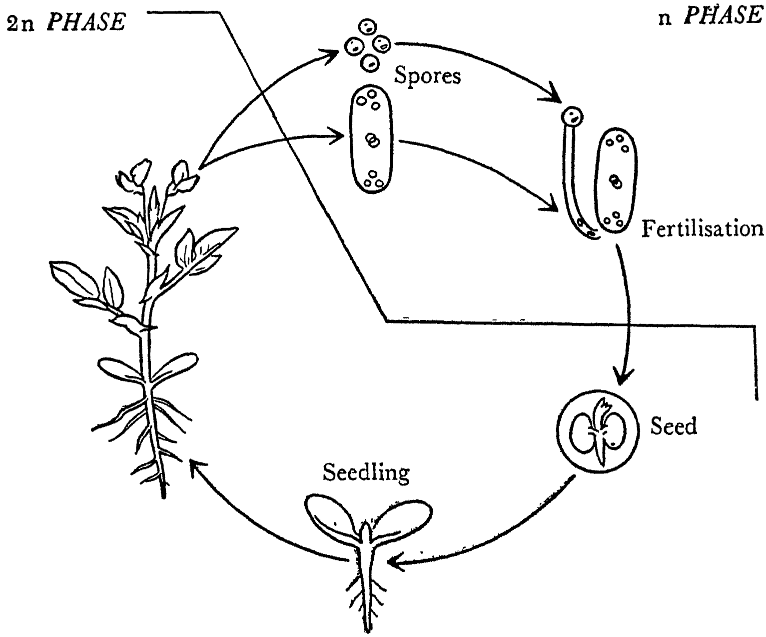


FIG. 180
A diagrammatic version of the life history of a flowering plant

of the new generation is represented by the embryo. The production of seed is regarded as the highest stage of evolution attained by plant life.

All other plants are lower in the scale; they produce no seed and are called, collectively, the *Cryptogams*. The highest cryptogams show relationship with the lowest spermophytes, for evolution is a continuous process and definite breaks do not often occur. "Missing links" are due to gaps in our knowledge rather than real gaps in the moves upward. Within the cryptogams, three main groups are recognized. (1) The *Pteridophyta*, which include the ferns, the horsetails, and their allies. (2) The *Bryophyta*, comprising the mosses and liverworts. (3) The lowest group, the *Thallophyta*, which embraces all the fungi and algæ.

The Ferns and their Allies: The Pteridophyta

Only in the higher pteridophytes are two kinds of spores produced; usually only one kind is formed. These are borne on modified

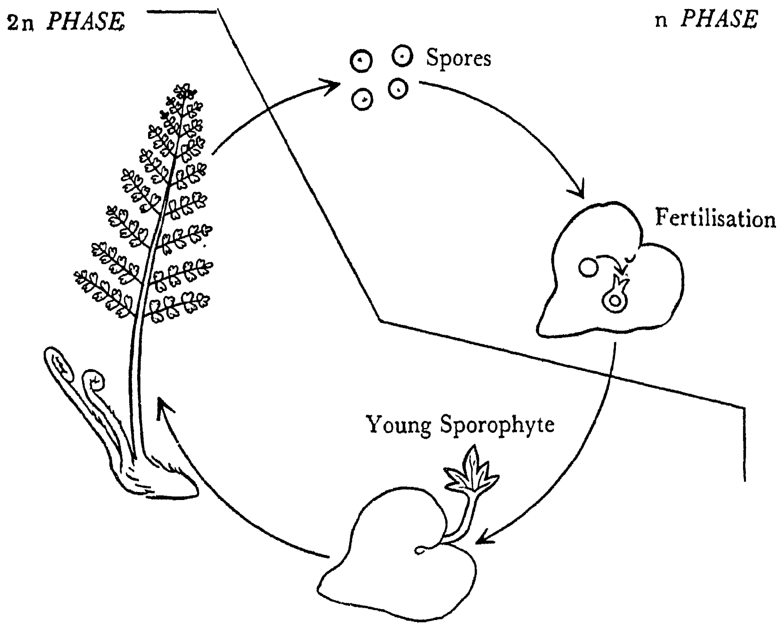


FIG. 181
A diagrammatic version of the life history of a fern

leaves arranged in cones as in the horsetail, or more usually on unmodified vegetative leaves as in ferns.

The fronds of the bracken fern show little groups of sporangia on the under surface in summer and autumn. In such a typical fern the spores are cast off from the parent plant and germinate under moist conditions. Each one develops into a small, green, heart-shaped body about an inch long which lies flat like a leaf on the soil surface. It is not differentiated into root, stem, or leaf, and is called a *thallus*. This little free-living plant before it dies produces only gametes. These fuse to produce a zygote, the start of a new sporophyte. There is thus a clearly marked alternation of generations in the fern.

The Mosses and their Allies: The Bryophyta

In the bryophyta, the same alternation is also clearly seen, but the ratio of size or importance of the two phases is quite different. The moss plant is the gametophyte, the sporophyte is a small, stalked capsule parasitic on the gametophyte. When these

groups are compared, it is seen that in the rise from the lowly moss to the flowering plant the gametophyte has become smaller and smaller and the sporophyte more and more dominant.

The Thallophyta

In the thallophyta, the lowest group of all, the whole plant is thallus, and what differentiation of parts there is, is of a very low order. The sexual processes are obscure and primitive. The thallophyta are divided into two groups : the algæ which possess chlorophyll, and the fungi which are without it.

Evolution commenced in the water. The thallophyta are largely aquatic; the mosses must be kept damp. The fern gametophyte at least needs liquid water. The angiosperm has overcome the problems of the dry land. As the plant progressed from the water environment to the land, there has been a progressive fall

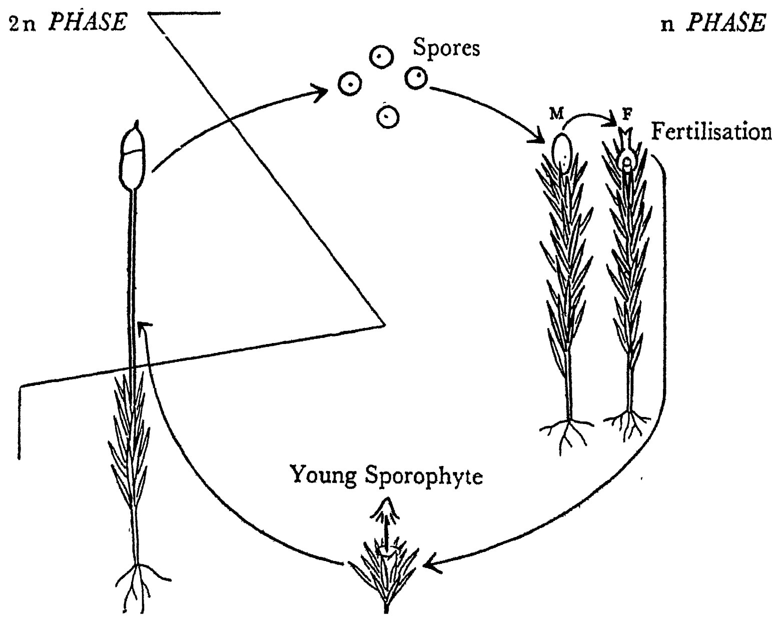


FIG. 182

A diagrammatic version of the life history of a moss

Compare this with Figs. 180 and 181 and note that in evolution there has been a progressive rise in the dominance of the sporophyte (2n) over the gametophyte

in the dominance of the gametophyte and a corresponding rise in the importance of the sporophyte. The sporophyte is the conqueror of the dry land.

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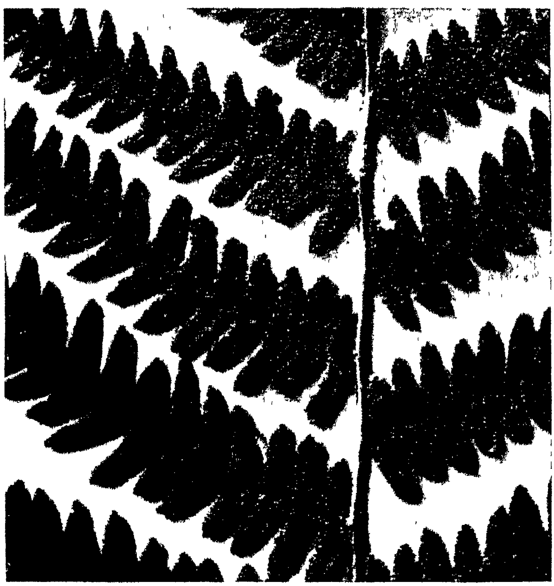
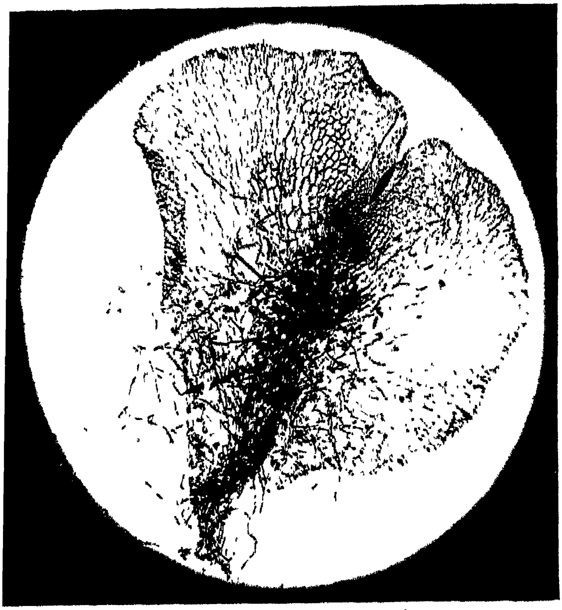
The megasporangia and seeds of a gymnosperm are not enclosed in an ovary ; they are exposed on a special leaf. The pollen develops on another special leaf and is carried by wind, etc., to this, the female

In the Fern only one kind of spore is produced. The sporangia are massed on the underside of the leaf which is used for photosynthesis. The spores are cast off and germinate on moist soil





The Fern spore germinates to produce a free living green thallus — the gametophyte. Sexual organs are massed on the central line

The Moss gametophyte is the small "leafy" portion seen at the base. Sexual organs develop at its apex. After fertilization the thin stalk with a spore-box at its apex—the sporophyte—develops. The sporophyte lives on the gametophyte

INDEX

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